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JOURNAL OF ANATOMY

A CONTRIBUTION TO THE MORPHOLOGY OF THE CORPUS STRIATUM

By RAYMOND A. DART,

Demonstrator of Anatomy, University College, London

INTRODUCTION

For a recapitulation of the essential features in the divergent conclusions of investigators who have studied this problem, we are indebted to the recent paper by Elliot Smith ('20) in which he pointed out the nature of the corpus striatum in *Sphenodon*, and indicated the morphological relationships of its several parts.

For some time past I have been studying a series of sections of the brain of the highly specialised Marsupial Mole, *Notoryctes typhlops*, which was very kindly placed at my disposal by Prof. Elliot Smith. As might be anticipated, in this creature devoid of any visual apparatus, the olfactory and closely associated striatal areas play a dominant rôle in its cerebral constitution—features already described by Elliot Smith in his communication to the Royal Society of South Australia ('95). In attempting to elucidate the significance of these structures I have investigated more primitive forms in the biological series; and I have to acknowledge the generosity of Professors A. Dendy of King's College and J. P. Hill of University College for the free access to their important collections, which has made possible an extensive comparative study. It is primarily for the purpose of abbreviating the account of the brain of *Notoryctes* that this preliminary note upon the striatal region is submitted; but the problem of the evolution of the corpus striatum is sufficiently important to call for this separate treatment.

If a transverse section of the brain of *Notoryctes* be studied in the region of the anterior commissure and foramen of Monro (e.g. A. 2. 7. of this series) (fig. 1), the pallial formation is recognisable as a continuous cell layer from the region of the fascia dentata and hippocampus dorso-medially, to the upturned lateral margin of the pyriform lobe ventro-laterally. Medial to this point (where the pyriform area is turned up to become continuous, through a scattered cell zone, with the denser structure of the claustral area lateral to the corona radiata) there are to be seen in section remnants of the lenticulo-striate artery (claustral artery of Shellshear, '20) whose significance as a guide to the morphology in this region has been indicated by Elliot Smith ('19). Medial to this vessel are to be seen the "scattered islands of Calleja"

E.M.T. 1-12-21

which constitute the "cortical" formation known as the tuberculum olfactorium. Medially this formation becomes continuous without any sharp break with the grey matter of the hypothalamic region—the constricting influence of the optic tract in strongly separating these two formations being absent in this brain.

It is important to recognise that the tuberculum olfactorium is a cap-like structure surrounding the enormously expanded striatal region ventrally.

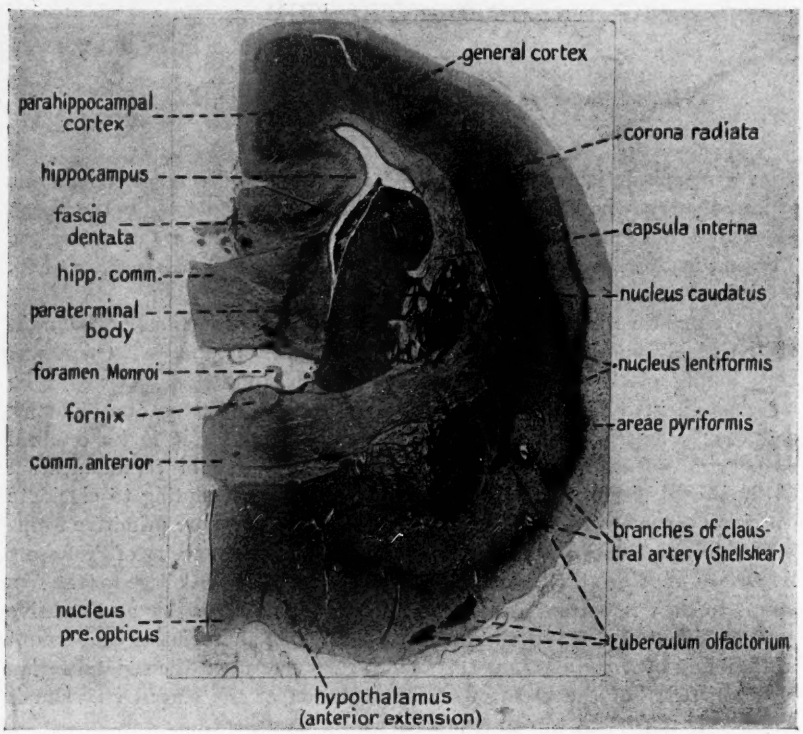


Fig. 1. Transverse section of cerebrum of *Notoryctes typhlops* (A. 2. 7. of this series) to show the scattered islands of Calleja and the lateral relationships of the tuberculum olfactorium.

Laterally this close relationship of Calleja's "islands" to the corpus striatum is preserved into the depth of the section as far as the anterior commissure, and indeed actual remnants of the tubercular cortex appear to be intermingled with the commissure itself. Certainly islets are to be observed deep to the lateral part of the claustral region and the upturned part of the pyriform lobe and the associated lenticulo-striate artery.

Ramon y Cajal (*Histologie du Système Nerveux*, tome II, 1911, p. 730) has remarked concerning this region: "Son aspect varie beaucoup avec

l'orientation et la place des coupes ainsi qu'avec l'espèce animale. Cet amas atteint ses plus grandes dimensions chez le chien, chez lui ses bords plongent jusque dans les couches profondes et projettes des cordons et des bandelettes ramifiées et anastomosées." Hence it is not to be wondered at if in a creature much more dependent for its livelihood upon its sense of smell than is the dog, an even more remarkable development of this component should be present.

Sagittal sections corroborate these observations concerning an apparently "inrolled" tubercular cortex: figs. 2 and 2 *a* (representing Section V. 2. 5. of this series) portray the same facts, viz., a pyriform cortex turned in above a

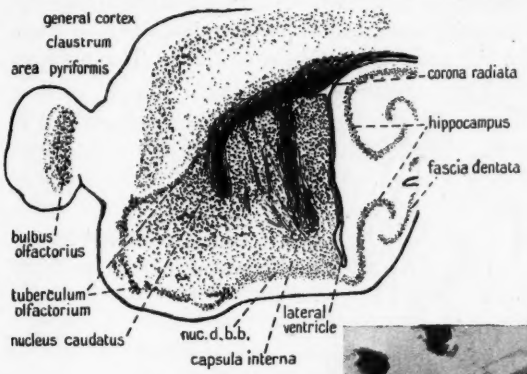


Fig. 2.

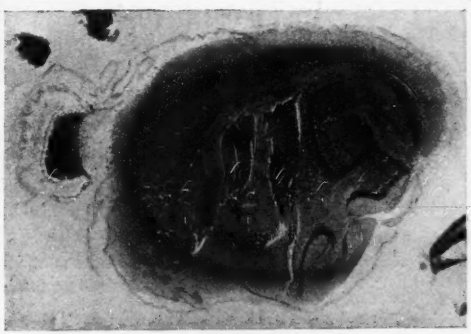


Fig. 2 *a*.

Figs. 2 and 2 *a*. Sagittal section of cerebrum of *Notoryctes* (Section V. 2. 5. of this series) to illustrate "embracing" relationship of the tuberculum olfactorium to the corpus striatum, and the continuous "cortical cap" of this body.

lenticulo-striate artery to become continuous with the claustrum, while below the artery the tubercular cortex is continued in its characteristic interrupted fashion till it meets the corona radiata and the anterior commissure.

Not every section illustrates these phylogenetic vestiges so diagrammatically as the two to which reference has been made; but despite the disturbing factors which have influenced the structure of this lowly Metatherian brain, a clear conception can be adduced of the primitive anatomical relationships of the region.

It is definite then that both ventrally, laterally, and anteriorly the tuberculum olfactorium in *Notoryctes* bears a definite "embracing" relationship

to the striatal region. The same longitudinal section (fig. 2) shows that this "cortex" is continuous posteriorly with a formation which is equally entitled to the appellation of "cortex," and later in this paper it will be proved to be composed of those elements known as the nucleus of the diagonal band of Broca (*nuc.d.b.b.*) and the amygdaloid nucleus.

Johnston ('13) has shown in detail the morphology of the tuberculum olfactorium on the medial side, his work being an extension of Beccari's ('11) results. In *Notoryctes* it is clear that in front of the region where it is continuous with the hypothalamus it forms the lateral boundary of the homologue of the preoptic nucleus (of many writers). Still further anteriorly it again penetrates deeply, separating the so-called paraterminal body (nucleus septalis of some writers) from the nucleus accumbens of Ziehen. This nucleus

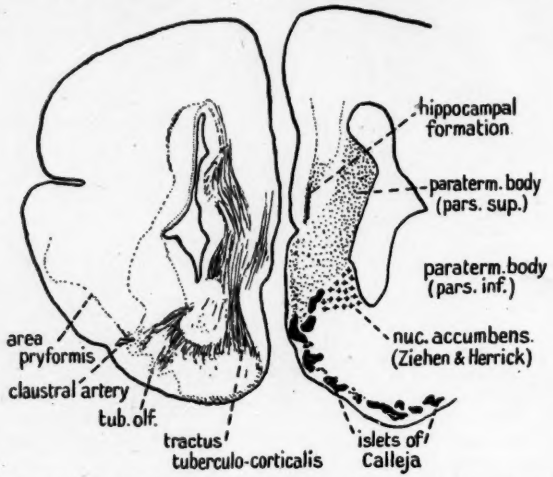


Fig. 3 (after fig. 27, Johnston, '13). To illustrate relationship of tuberculum olfactorium medially, anterior to the commissures.

accumbens is a portion of the palaeostriatum, and it is therefore separated from the paraterminal region by islets of Calleja. This is clearly portrayed in Johnston's ('13) figures one of which I reproduce here as fig. 3 depicting the state of affairs in *Didelphys*. While her specimens obviously (e.g. her diagrams 6, 7 and 8) illustrate this cell grouping, Crosby ('16–'17) does not recognise the patent fact. The confusion which obtains in the nomenclature of this region is a token of the uncertainty concerning its interpretation. The tubercular formation is not well developed in Reptilian forms and it is curious that where its islet formation is clearly marked, viz., in the cortical islets capping the anterior end of the palaeostriatum (the caudate nucleus of Johnston in the turtle, '15), writers (such as Johnston, '15, and Crosby, '17) should choose to dignify it with the distinctive title of anterior olfactory nucleus. No useful purpose can be served by unnecessarily

adding to the already unwieldy and cumbersome accumulation of anatomical terms. The structure in question is merely the most obvious portion of the tuberculum present in Reptiles.

Before entering into the discussion of the morphology it is necessary to refer to a further conclusion insisted upon by Johnston ('13), and previously recognised by Elliot Smith (e.g. '02). This is the careful discrimination between a supra- and infra-foraminal portion of the paraterminal body (or commissure bed) of Elliot Smith (see fig. 5). This discrimination has unfortunately led to the use by Johnston of the term "primordium hippocampi" invented by Elliot Smith for a wholly different structure. Whether, as he contends, there is any justification for this gratuitous transference of terminology and incidental confusion remains to be proved. Apart from the question of priority of usage, the appellation "primordium" as applied to any structure is meaningless unless that structure gives rise later in phylogeny to the tissue of which it is called the primordium. And this Johnston has failed to show. For the purposes of this paper I prefer to use the terminology of Elliot Smith. It will therefore appear that the infra-foraminal portion of the commissure bed corresponds with the medial parolfactory nucleus (so-called) which is stated to meet its fellow of the opposite side in the nucleus of the anterior commissure, and is continuous behind with the nucleus preopticus. I am not wholly in accord with the interpretation of the cell masses found by Röthig ('12) in this region: otherwise I would gladly have utilised his terms "pars dorsalis et ventralis."

THE ORIGIN OF THE HYPOPALLIUM

The brain of *Lepidosiren* presents with almost diagrammatic clearness the simplest arrangement of cortical cell groupings in the cerebrum. In the absence of definite knowledge concerning the arrangement of its fibre tracts our interpretation of its forebrain is not yet conclusive. It has been described by Elliot Smith ('08). Figs. 4 and 5 have been taken from his work, in which the double constitution of the commissure bed was pointed out. This conclusion has been questioned by Herrick ('10). Apart from this however, there are two outstanding characteristics of its forebrain which merit special attention in a study of the striatal region. The first relates to the tubercular cortex, which is seen (figs. 4 and 5) completely to surround a cellular area ventral to the ventricle. This cellular mass below the ventricle is the palaeostriatum (of Kappers) and, as has been shown by various authors, its limits are indicated by sulci in the ventricular wall; that is to say, the sulci are opposite the medial and lateral limits of the tubercular cortex.

The primitive morphological relationship for the vertebrate palaeostriatum then, is that it should lie within a cortical structure, which we may term provisionally the "palaeostriatal cortex," a portion of which we recognise as the tuberculum olfactorium. This tuberculum olfactorium is a very obvious

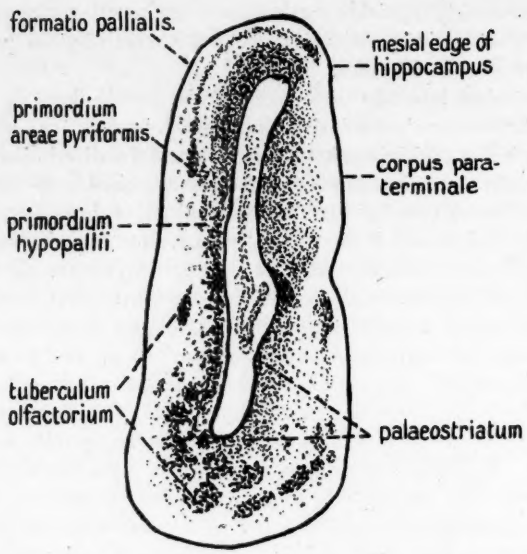


Fig. 4. A coronal section through the left cerebral hemisphere of an adult *Lepidosiren paradoxa* Fitz., a short distance in front of the lamina terminalis (Graham Kerr's section 148 c. 37. 2.). × *circa* 10. (Reproduced from Elliot Smith's paper on "The Cerebral Cortex in *Lepidosiren*.")

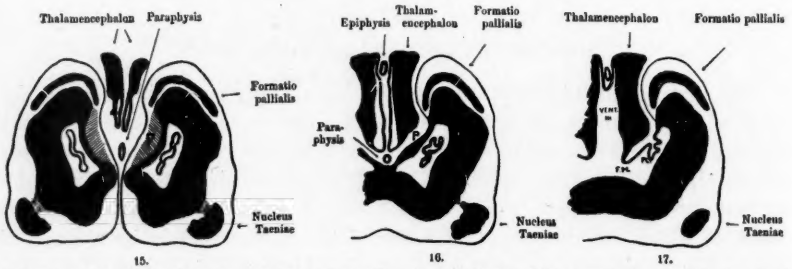


Fig. 5 consists of the three figs. 15, 16 and 17 taken from Elliot Smith's article upon "The Cerebral Cortex in *Lepidosiren*," and here reproduced to reinsist upon his interpretation of the para-terminal region in that form and to show the relationship of the "nucleus taeniae" so-called to the palaeostriatal region. His description of the figs. is appended.

Fig. 15. A diagram of another section (20. 2. 4.) of the same series cut immediately in front of the lamina terminalis. (140 A. 20. 2. 4.) × *circa* 20.

Fig. 16. Here the lower parts of the paraterminal bodies have fused to form the commissure bed or matrix for the cerebral commissures. The dorsal portion of the paraterminal body, marked *P* in fig. 15, has now become attenuated to form an epithelial membrane *P*. (140 A. 20. 3. 6.) 70 μ behind the section represented in fig. 15.

Fig. 17. Diagram of a section 40 μ behind that shown in fig. 16. (140 A. 21. 1. 2.) The paraterminal lamella (*P* in fig. 16) has now given place to the lamina chorioidea, which is invaginated into the lateral ventricle to form the choroid plexus (*PL.*).

F.M. Foramen of Monro. *vent. III* third ventricle.

feature in certain fishes, and also as we have seen in Mammalia, but may be inconspicuously developed in certain reptilian forebrains. But the palaeostriatum is always enclosed by a cortex of some kind; and I find myself in strong disagreement with the statements of certain authors (e.g. Johnston, '15) who find that the striatal areas are sometimes covered by, and sometimes free from, a migrating olfactory area. The palaeostriatum presents a typical arrangement throughout the vertebrate series, it is encapsulated by a "palaeostriatal cortex." Hence it is apparent that the tubercular cortex found in *Notoryctes* represents the remnants of that completer arrangement shown in primitive vertebrates such as the Dipnoi.

A second characteristic to be noted in the Dipnoan cerebrum (cf. fig. 4) is a certain area of cortex lying between the lateral boundary of the so-called "formatio pallialis" of Elliot Smith and the lateral boundary of the tuberculum olfactorium. It conforms to all the known criteria of the region called "hypopallium" by Elliot Smith in reptilian forms: for it lies between the above-stated regions and already shows a "bending-in" which has affected the contour of the ventricular wall. It is the part of the primordial cortex first to be affected by the stimuli arriving from diencephalic centres, and by neurobiotactic influence comes to assume a deeper position. It may be regarded as the forerunner of the claustrum and part of the corpus striatum of still higher forms, and is therefore the "primordium hypopallii."

In this communication I have deliberately refrained hitherto from discussing the Elasmobranch forebrain (which is perhaps the most unspecialised primitive vertebrate form known to us) because that structure has been analysed by Johnston ('11). I intend at a later date to give an account of the Selachian forebrain in which I shall enter into a detailed criticism of that author's conclusions, but in this communication I shall refer only to certain points directly relevant to the matters under discussion here. *Lepidosiren* presents us with an indubitable homology on account of the macroscopical clearness of its tuberculum olfactorium, its definite relation to the simple palaeostriatum and the obvious meaning of the remaining cell masses.

Exactly the same formations are, however, to be seen in the Selachii and even in the specialised and retrogressive Amphibia. A comparison of Johnston's own figures ('11 and '13), and the distribution of the cell areas as depicted by J. Stuart Thomson ('18–'19), with fig. 6 will disclose this fact unappreciated by either of these authors, which is all the more remarkable since Röthig had pointed out this "rudiment of the epistriatum" in 1912. After discovering this rudiment as figured in his paper ('12), it is surprising that Röthig himself should have had any doubt concerning the cortical nature of the epistriatum (cf. his figures for *Hynobius*, *Cryptobranchus*, etc.). Prior to my examination of the *Lepidosiren* cortex I was quite unaware of Röthig's facts, and although there is not in the Amphibia (owing to its retrograde development) the same degree of cortical differentiation that one finds in the Dipnoan, the homology of the several parts is precise and unquestionable.

Preparations of the Selachian forebrain stained by the Weigert or Bielschowsky methods exhibit the nature of the factors actually at work in the production of this so-called "Epistriatum-Anlage" or as I have already named it "primordium hypopallii." In a transverse section (stained by the Weigert method) through this brain in the region of the distribution of the lateral olfactory tract (fig. 7) it will be seen that, medial to this nucleus of

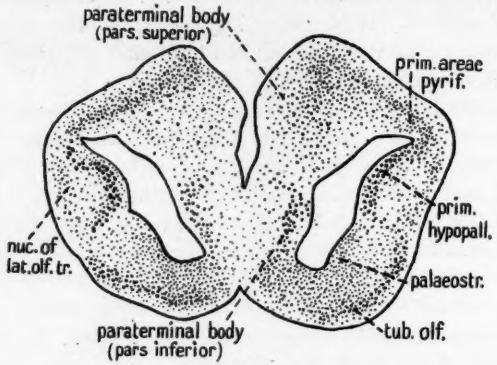


Fig. 6

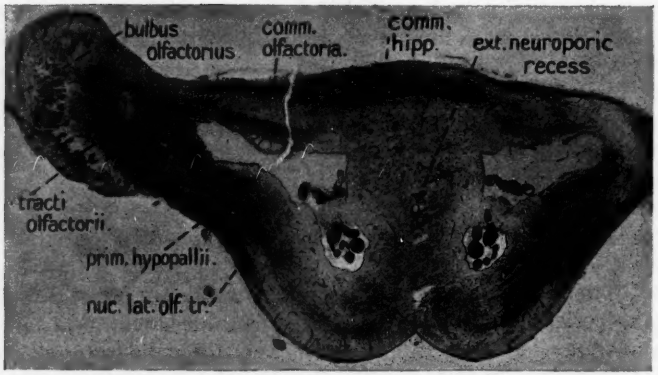


Fig. 7. Actual photograph of a transverse section of cerebrum of *Scyllium* (prepared by the Weigert method) to demonstrate the distribution of the fibre tracts in the region. *comm. olfactoria* = the so-called "corpus callosum" of Johnston.

the lateral olfactory tract (*nuc.lat.olf.tr.*) there is a mass of fibres which have a different direction, for they course upwards and laterally, as if issuing from the main forebrain bundle, and are distributed to an area abutting upon the ventricular wall and forming the hypopallial ridge.

If the cell masses of the same form are now considered in the light of what has already been shown it is clear from fig. 6 (copy of lantern slide taken from

an actual photograph by Elliot Smith) and figs. 8 and 9, which show the distribution of the cell masses in an embryo of *Scyllium*, that the ventral part of the forebrain is a palaeostriatum ensheathed by a definite cortex, which is the tuberculum olfactorium, although the typical "islet" formation is not very characteristically developed, probably owing to its primitive lack

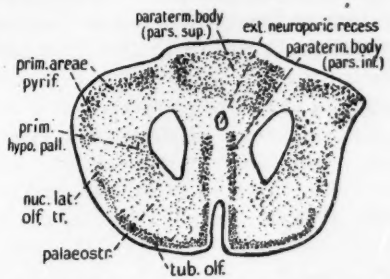


Fig. 8. Transverse section of cerebrum of developing *Scyllium* anterior to third ventricle to illustrate the cell-mass distribution.

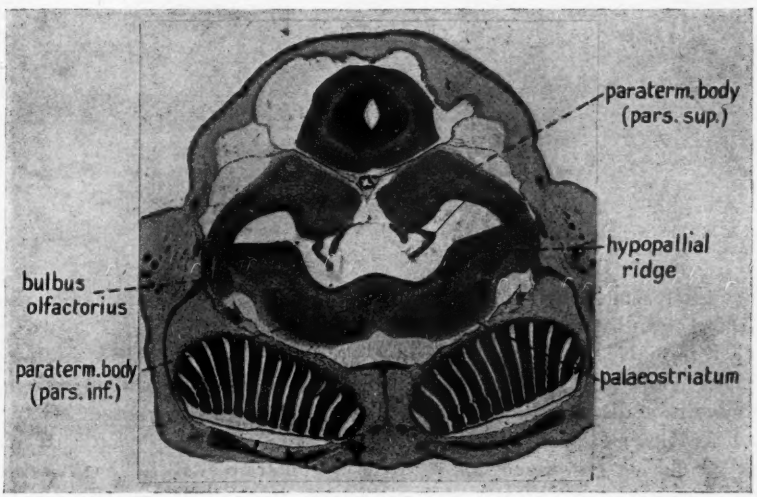


Fig. 9. Photograph of transverse section of developing *Scyllium* in region of attachment of the olfactory bulb. Note nucleus of lateral olfactory tract and the hypopallial ventricular bulging lateral to the palaeostriatum which is covered by the tubercular cortex.

of differentiation. Immediately lateral to the limits of this palaeostriatum, as indicated by the ventricular sulcus, there is a bulging in of the ventricle corresponding to a cellular mass continuous dorsally with the pallial formation. But this very definite cell mass lies deep to a cortical differentiation, which is the cellular area serving as the receptive nucleus of the lateral olfactory

tract as we have already observed. The distinctive nature of the structures referred to is thus shown diagrammatically in the foetal brain (figs. 8 and 9) where the disturbing influence of the developing tracts has not, as yet, reached its full expression. The common point where the primordium hypopallii and the lateral olfactory tract nucleus meet the pallial formation dorsally is to be recognised as the primordium of the pyriform lobe of higher forms. The deduction that we have in *Scyllium* the beginning of that process of a "dragging in" of a cortical structure to form those portions of the striatal complex known as the hypopallium in reptiles is obvious, and we have further an ocular demonstration of the activity of the factors in that process, viz., a superficial set of impulses (lateral olfactory tract) retaining at the surface (on Äriens Kappers's principle of neurobiotaxis) a cellular layer clearly definable as the nucleus of the lateral olfactory tract, and a deep set of impulses coming in by way of fibres closely associated with the forebrain bundle, which, attracting the deeper cortical cells towards the source of their stimulus,

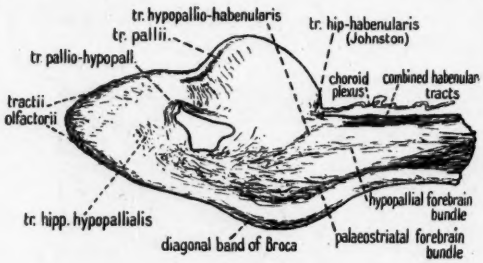


Fig. 10.

Fig. 10 *a*.

Fig. 10 *a*. Photograph of the section from which fig. 10 was drawn to show the relation of the diencephalon and mesencephalon to the cerebral hemisphere in *Scyllium*.

cause the formation of the ventricular bulging, in a way exactly homologous to that shown by Johnston for the turtle ('15).

The probable source of this deep set of fibres associated with such an important modification of the originally simple pattern of the pallium will undoubtedly be discovered by a fuller study of the Selachian brain. My own studies of three series of specimens stained by the Weigert method, (transverse, sagittal and horizontal) controlled by the examination of Bielschowsky series, have convinced me that the forebrain bundle in *Scyllium* has two distinct components; one is the ordinary basal bundle constituents, which has long been recognised, while the other concerns the most dorsal and lateral portion. In both sagittal (fig. 10) and horizontal (fig. 11) series, this element of the forebrain bundle is seen to be quite distinct from the basal portion and its goal has been determined as the region I have described as the hypopallial primordium. I have no doubt (from my series) that it is a dorsal thalamic tract and it seems also to receive accessions direct from the tectum opticum. These accessions correspond with the "strio-tectal" tract found

by Franz ('12) in various bony fishes. Johnston has described in the Selachian forebrain a so-called "somatic area," and Judson Herrick accepts this reading, as is shown by his retention of this conception in his *Introduction to Neurology*—though elsewhere ('17) he has recognised the striatal nature of Johnston's "somatic area." I have been unable to find any specialised area corresponding with Johnston's description, and more particularly I cannot admit that the structure defined by him is the special site of termination of the more recent thalamic and tectal tracts that appear in this cerebrum. Undoubtedly the hypopallial formation extends a long way posteriorly; but it can everywhere be distinguished from such unrelated elements as the tractus taeniae, which Johnston also traces to his "somatic area." But this and other divergent results I shall discuss in a future com-

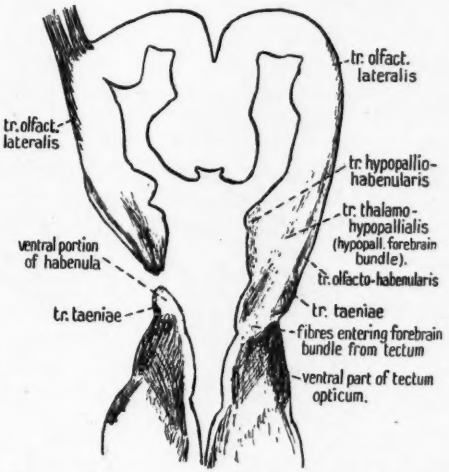


Fig. 11. Diagram of horizontal section of brain of *Scyllium* to illustrate in particular the afferent and efferent paths of the hypopallial primordium.

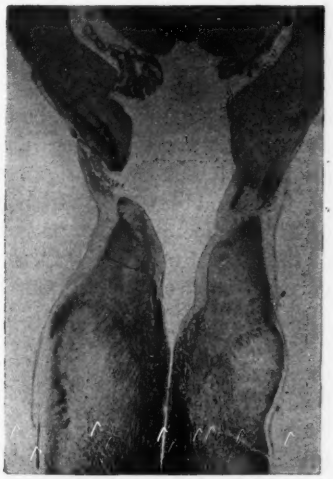


Fig. 11*a*. Actual photograph of the section from which fig. 11 was drawn.

munication. That the recognition of the fallacy of these views is of crucial importance is evident from an examination of the deductions made by Johnston from his data. He has reopened the classical dispute concerning the presence of callosal fibres in the hippocampal commissure, and in support of his thesis has claimed to have discovered a so-called "corpus callosum" in the Selachian forebrain. A study of his diagrams (or better still actual specimens of Selachian brains) will show that the fibres he has termed callosal take their origin in an area including the lateral olfactory tract and the lateral part of the tubercular cortex. I have therefore termed it the *commissura olfactoria* (see fig. 7). Specialised commissural connections of these primitive olfactory regions cannot be homologised with a structure so dissimilar functionally as the corpus callosum. This is derived from the neopallium

which is not yet differentiated in fishes. As we now know, the neopallium appears definitely for the first time in the Reptilia and the site of its origin is closely related with the anterior end of the hypopallial region. The appearances in this particular part of the Selachian forebrain are highly interesting and suggestive of a foreshadowing of the neopallium: but their consideration will have to be deferred to my later communication. Meantime it is to be recognised that this anterior extremity of the hypopallium has no relationship whatever to Johnston's fictitious "corpus callosum."

THE FATE OF THE NUCLEUS OF THE LATERAL OLFACTORY TRACT

Reference to figs. 6 and 8 shows how this nucleus bears a very precise relationship to the hypopallial primordium. This is an anatomical arrangement concerning the nature of which I was for a long period greatly exercised, seeing that Elliot Smith had described the continuity of the hypopallium with the pyriform cortex, but had not entered into other problems concerned in the process of evolution of the striatal complex. The study of the tract-distribution has however given the clue, and obviously the study of the cerebrum of *Sphenodon*—in order to understand what had become of this lateral olfactory nucleus—was of considerable moment. Owing to the liberality of Prof. A. Dendy I had the opportunity of studying the development of its striatal complex. This study revealed a continuous series, from the simple form resembling the condition found in the Selachian brain to the fully developed adult described by Elliot Smith. During development (e.g. fig. 12) there is to be recognised a small, though definite rudiment of this nucleus perforated by the lenticulo-striate artery, and even in the adult *Sphenodon* some scattered nuclei, representative of this primitive structure, are to be recognised. In the course of his paper ('20) Elliot Smith corrected his earlier conception and pointed out that the lateral edge of the pyriform primordium is continued into the hypopallium "without any disturbance of the superficial layer of the pallium, which still remains in unbroken continuity with the surface of the palaeostriatum, but without the intervention of any furrow." It will be seen that my interpretation of the facts (as illustrated by this comparative study) is that the infolding of hypopallium is merely the expression of an exuberant

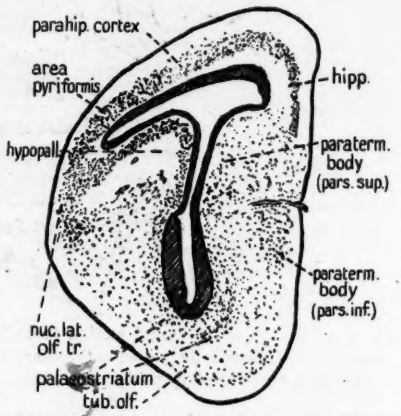


Fig. 12. Transverse section of brain of *Sphenodon* (stage F) to show condition of the nucleus of the lateral olfactory tract (*L.O.T.*) at this stage.

growth of the internal layer of the "primordium hypopallii" in the Reptilia, which has caused a bulging inwards of the ventricular wall, while the unbroken contour of the surface is merely the exhibition of the influence of the fibres of the lateral olfactory tract in keeping a small cellular layer at the surface.

It would have been unnecessary to have emphasized this fact were it not that many Reptilia fail to demonstrate the diagrammatic "cortical" continuity of the hypopallium of *Sphenodon*, or of *Lacerta* as figured by De Lange. It is apparent from the study of the turtle (Johnston, '15) and the alligator (Crosby, '17) that there are in these forms certain anomalous conditions of the striatal complex not easily reconciled with that of more archaic forms. The same is true of the striatum in snakes and monitors. What the exact explanation of all the forms of striatum exhibited by these families is we are not yet in a position to say. In some reptiles, such as *Varanus* (e.g. Elliot Smith's paper, '20), there is a very diffuse scattering of the hypopallial cells, in others it does not seem unlikely that there is a spreading out laterally of the palaeostriatum, to separate the hypopallium and the nucleus of the lateral olfactory tract (Johnston, '15); and in these it would seem that the division of the original cortical cell mass and the entrance of the fibres causing the differentiation of the hypopallium, have supplied the path for the spreading referred to. Further, much of the complexity of this interesting site is to be understood, when it is recognised that the adjacent superficial areas (pyriform lobe, superficial layer or nucleus of lateral olfactory tract, and tuberculum olfactorium) are subject to the influence of identical stimuli—hence a tendency to closer grouping of the masses, and homogeneity of structure, with an obscuring of the phylogenetic landmarks. That the embryological history, however, depicts the several stages in the phylogenetic development of these structures has been demonstrated by Elliot Smith even for man.

THE AMYGDALOID COMPLEX

With the historical aspect of this problem I do not intend to deal, for it has been well summarised by Völsch ('06) who has pointed out the conclusions arrived at by Meynert ('67), Mondino ('85), Ganser ('82), Honegger ('90), Ziehen, Kölliker, Cajal and other observers whose researches are for the most part restricted to the mammalian orders. In 1867 Meynert insisted upon the close relationship between the claustrum and the amygdala, but despite our advance in knowledge of the fibre tracts and the means of investigating them, the amygdaloid complex has remained unravelled.

To keep the issues clear, this division of the corpus striatum is considered separately. The first striking observation in regard to this portion of the striatum in *Notoryctes* which confronted me, was that in any typical section of the region (e.g. fig. 13—Section C. 3. 5. of this series) there was very definite evidence of a "cortical" layer of cells covering all parts of the corpus striatum, including the region known as the amygdala. Further the amygdaloid complex

has a very definite location between the hippocampus medially and the pyriform lobe laterally, and the transition from subiculum to amygdala is not very apparent. From Johnston and Crosby's descriptions it is obvious that essentially the same relationships hold good for this region in the turtle and the alligator, where the so-called amygdala is treated as a complex of the homologue of the nucleus of the tractus pallii (in fishes) together with the projection tracts of the lateral olfactory nucleus and pyriform lobe. The homology of the tractus pallii with a specific portion of the stria terminalis (olfactory projection tract of Cajal) may be regarded as established. It will therefore be evident, that if the homologues of the various components of the amygdaloid nucleus of higher forms can be isolated in the Selachian forebrain, we are in a position (owing to the definite homologies existing between the reptilian and mammalian forebrain) to explain the mammalian modifications.

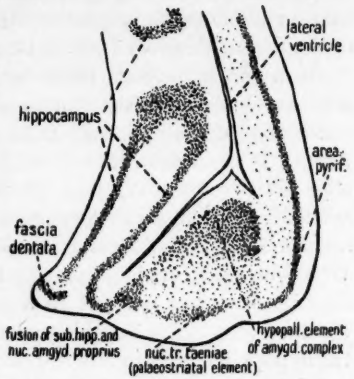


Fig. 13. Ventral half of a transverse section. (C. 3. 5. of this series) of the cerebral hemisphere in *Notoryctes typhlops* to illustrate the components of the amygdaloid complex at this level.

THE ELEMENT *A*

The destination of the tractus pallii in the Selachian forebrain is the posterior and lateral part of the roof of the forebrain. Its situation is very definite—between Johnston's "primordium hippocampi" medially and the primordium of the pyriform lobe and nucleus of the lateral olfactory tract laterally—in short it corresponds with at least part of the region I have indicated in *Notoryctes*. This cortical area in *Scyllium* (fig. 14) is situated very deeply abutting upon the dorso-lateral aspect of the "posterior arm of the ventricle" and is to be distinguished by the shower-like appearance of the fibres of the tractus pallii as they pass in from the superficial tract. It is to be noted that the region is quite separate from and unrelated to the other elements grouped with it in higher forms

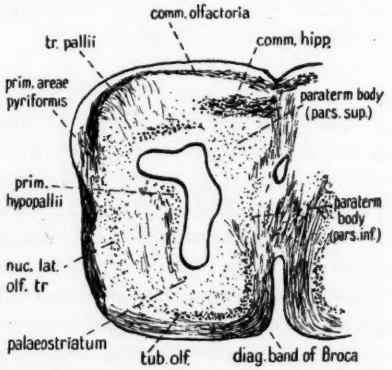


Fig. 14. Transverse section of cerebrum of *Scyllium* (adult) to show the distribution of the tractus pallii and the situation of its nucleus. Drawn from specimen stained by Bielschowsky method.

as the "amygdaloid complex." In this posterior part of the forebrain (cf. fig. 9) the palaeostriatal region is mainly occupied by the forebrain bundle, and is continuous with its fellow of the opposite side through the nucleus preopticus. The hypopallium is relatively small, and is found to be the site of origin of a descending tract. But its cellular layer is continuous laterally with the region into which the tractus pallii discharges. The posterior limits of the pyriform and lateral olfactory tract elements are hard to distinguish, but these with the palaeostriatal cortex of this region (i.e. the nucleus taeniae) are the site of origin of important habenular connections.

Practically the same arrangement is found by Johnston for the turtle, and *Sphenodon* presents a diagrammatic relationship of the constituents in this region (fig. 15) the hypopallium and nucleus tracti pallii (*Sph. I.* 33. 1. 3) still preserving their ventricular position and their relationship to one another and to the hippocampus. The isolated character of "the large-celled medial

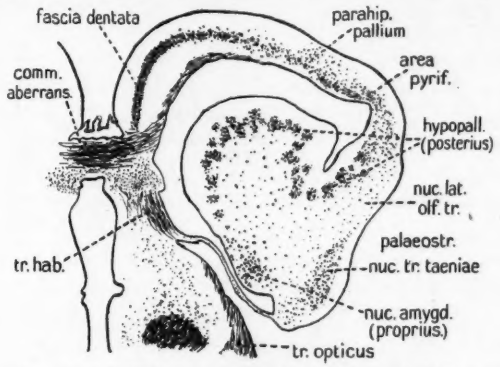


Fig. 15. Lateral section of adult *Sphenodon* to illustrate the morphological relationship of the amygdaloid complex. See text. (Dendy's series *Sph. I.* 33. 1. 3.)

nucleus" constituent of the complex has been insisted upon by Johnston in his description of the cell masses in the turtle. It may be referred to as the "amygdala proper" (Johnston's medial large-celled nucleus, Crosby's ventro-medial nucleus—though the latter author's failure to separate the subiculum hippocampi from the ventro-medial nucleus, throws some doubt upon the exactitude of her delimitation of this region). At the same time, Johnston's identification of the medial large-celled nucleus in diagrams 15 and 16 in his paper ('15) is incorrect. This region is not a portion of the amygdala proper, but is the palaeostriatal cortex, here quite distinct, and as is evident in fig. 15 of this paper, forms the nucleus tracti taeniae.

In their *Anatomical Guide to Experimental Researches on the Rabbit's Brain*, Drs Winkler and Potter (fig. xi, reproduced here as fig. 16) have identified three separate cell-masses lying in the space between the pyriform lobe and the tractus opticus, terming them respectively the nucleus amygdalae, subiculum cornu ammonis and zona presubicularis.

This complex has also been the subject of an extensive and painstaking research by Max Völsch ('06 and '10–'11): but, as his investigations were limited to the Mammalia, he found little more than a progressive differentiation in this area when traced through the series. His work has been of significance however in determining that for all mammals the amygdaloid complex can be roughly divided into the three components outlined by Winkler and Potter and insisted upon in this paper.

Accepting then the fundamental division of the complex into three regions, it is the "zona presubicularis" of Winkler and Potter or "basaler

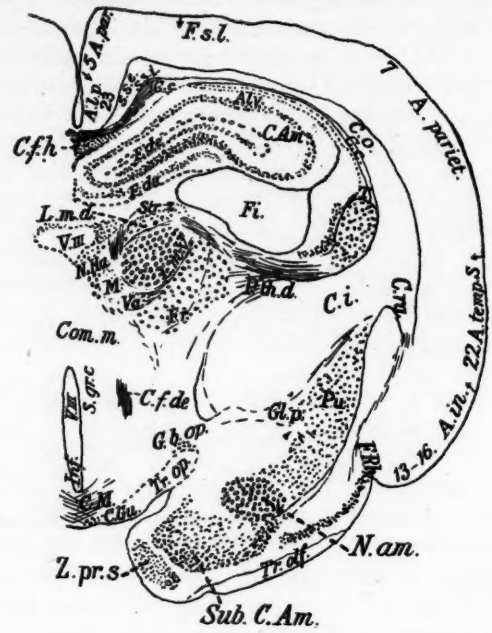


Fig. 16

Spitzenkern" of Völsch that corresponds with the "large-celled medial nucleus" of Johnston (amygdala proper) and seems to be the homologue of the nucleus of the tractus pallii in fishes.

It is well to recollect that Cajal (p. 723) states for mammals that: "Le noyau amygdalien (the amygdala proper) émet très certainement des fibres qui vont au taenia (semicircularis) mais jusqu'à présent il nous a été *impossible de constater le fait* de visu." Further, although Kölliker ('96) regarded the tract of the so-called taenia semicircularis as arising from the pyriform lobe, lenticular nucleus and amygdaloid nucleus, he nevertheless considered it as an annex of the striatal region, and not an olfactory tract of the third order as did Déjerine. Kölliker's interpretation agrees with Cajal's. Two points

concerning Cajal's observations are of the highest importance in the present discussion. First, that direct olfactory tracts never enter the amygdaloid nucleus proper, and second, that he was unable at any time to find a portion of the taenia semicircularis fibres *arising* from its cells, although he carefully searched for such a constituent. He did however believe that some fibres arose from the "cortical" part of the amygdala proper and entered the taenia.

There is no doubt that the one and only area conforming to such a criterion in the Selachian forebrain is this area of distribution of the tractus pallii. The tractus pallii takes origin in the hypothalamus in the cells lining the walls of the large tuber cinereum of these forms, and after extensively decussating just behind the optic chiasma travels partly superficially to, and also amongst, the optic tract fibres to take up a position laterally in the telencephalon medium, until it is distributed (in the manner described above) to the dorso-lateral part of the posterior portion of the telencephalic wall and roof.

Kappers and Theunissen ('07) and Kappers and Carpenter ('08) have confirmed the important finding of Wallenberg by a study of degeneration experiments, that "there is one ascending hypothalamic bundle, and one only to the forebrain of animals with a normal forebrain."

Johnston indeed ('09) states that the "tractus lobo-epistriaticus in fishes is believed to carry up gustatory impulses to the epistriatum from the tertiary gustatory centres in the hypothalamus," and has therefore concluded "that the 'epistriatum' must be regarded as a correlating centre for smell and taste and so be a forerunner of the smell-taste cortex." This use of the unfortunate term "epistriatum" can only be deplored, for by the "tractus lobo-epistriaticus" Johnston undoubtedly refers to the one definite tract associating the hypothalamus with the cortex, and this in fishes is the tractus pallii. In Reptilia and Mammalia it is a very definite constituent of the taenia semicircularis which goes to a restricted portion of the so-called "amygdaloid complex"—it is the nucleus amygdalae proper.

There must be some fibre tract which carries into the vertebrate forebrain those impulses, which, when transmitted upwards from their receptive nucleus in the medulla oblongata, are interpreted as sensations of taste. Such a component in the forebrain of fishes would necessarily be large, as taste is one of their dominant senses. Seeing that the tractus pallii is the only ascending tract from the hypothalamus to which Herrick has traced relays from the primary gustatory end nuclei in the medulla, the inference is justifiable that the primary importance of this tract in fishes and the persistence of its homologue throughout the vertebrate series, is due to this function which it subserves. In the Selachian, there is a large correlation bundle connecting the area of distribution of the tract possibly with the hippocampus and certainly with the anterior end of the hypopallial formation. It may be that this latter region is the primary seat of those disturbances which presaged the birth of the neopallial primordium.

Landau ('19) has pointed out that even in the human brain the cells of

the nucleus amygdalae are continuous with those of the hippocampus. This is certainly true in Selachians and the reptiles and hence there is a further link here in the chain of phylogenetic evidence. He states that there is a tract connecting the two, and though this may be the case in the Selachian brain, the most apparent connection of the amygdala (nucleus tracti pallii) anteriorly is with the anterior end of the hypopallium (see fig. 10, tractus pallio-hypopallialis).

If the tractus pallii is the bearer of those impulses which are interpreted as sensations of taste in the cerebrum, we are justified in interpreting the amygdaloid nucleus proper and the amygdaloid tubercle associated with it (first named by Kölliker in the rabbit), as the site where these afferent impulses terminate in the mammalian brain.

The superficial position of this element of the complex, which the work of Völsch has shown to have little or no relation to the ventricle in most mammals, calls for some explanation. Indeed he has named it the "basaler Spitzenkern." Apart from those stresses operating in this region, to which I shall be later drawing attention, two facts are to be noted; first, that the nucleus is under the neurobiotactic influence of a superficially placed tract (tractus pallii), second, that Völsch himself has shown how pure mechanical factors of growth can result in the movement of large areas (his nuclei *M* and *T*) from a ventricular situation. It is of some significance that Völsch was unable to confirm the statement of Ganser "that there is a contribution from this nucleus to the anterior commissure," and further that he, too, could not determine whether it was an efferent nucleus. Such then is the status of the element *A*, which may also be termed the "pallial element" of the amygdaloid complex.

In putting forward this hypothesis I am not unaware of the contentions of the American School of neurologists. Far from being deterred by the "epistriatal" hypothesis (of '09) to which I have already referred, they have insisted that taste impulses are carried to the forebrain in the medial forebrain bundle by a tract as yet undiscovered, that this tract discharges into the hippocampal formation, and therefore the hippocampus, being connected by relays of neurones with so-called "visceral" centres in the lower parts of the brain, is an olfacto-visceral correlation centre. Smell is claimed to be a "visceral" sense; and so, in contradistinction to a so-called "somatic" cortex, the American neurologists refer to a "visceral" representation in the cerebrum. These series of gratuitous assumptions are so utterly devoid of any justification that it hardly seems worth while to embark upon an exposure of their fallacy. By the method of argument adopted by Johnston—classifying any mass connected by a fibre tract directly or indirectly with a visceral or somatic nucleus—it would be possible to present a case for the view that any part of the central nervous system whatsoever was either visceral or somatic, as it suited the predilection of the arguer at the moment. In many fishes the taste buds are ectodermal, and satisfy all the requirements of an

exteroceptive sense. At most, a taste-organ is a borderland mechanism which, although the balance of evidence may be in favour of such a conclusion, cannot be definitely accepted in the present state of our knowledge as visceral. Finally if the reasoning adopted leads not only to this assumption and those already mentioned, but also, when we have traced our "visceral" relays into the cerebrum, exercises its magic to such a degree as to make us interpret a thorough-going somatic, ectodermal and exteroceptive sense (viz., smell) as a specialised visceral sense, the limit of paradox is undoubtedly reached.

Roughly outlined, this is the obscurantist aspect of the above hypothesis, which has led to the search for a somatic cortex where it did not exist and has created difficulties that have prevented the appreciation of the full significance of the neopallial primordium. The names "visceral" and "somatic" reduce forebrain terminology to an absurdity, and should be completely discarded if the issues are to remain unclouded.

THE ELEMENT *B*

The second element in the constitution of the so-called amygdaloid complex is a cortical layer of cells which includes the nucleus of the diagonal tract of Broca, which in Selachians and even in *Ornithorhynchus* seems inseparable from the cortex I have termed tubercular (Johnston's area superficialis basalis). This tract travels antero-medially to be distributed to the paraterminal region. The remaining constituents of this element are the areas of origin of efferent tracts such as the cortico-habenular tracts (which are represented in *Scyllium* by efferent tracts first from the posterior part of the "primordium hippocampi" of Johnston, second from the nucleus of the lateral olfactory tract, and third the tractus taeniae, which, arising from a specialised part of the postero-lateral portion of the tubercular cortex adjacent to the optic chiasma, passes dorso-posteriorly (the most lateral structure in this region of the telencephalon medium) and runs to the habenula. It is to be recognised that the anterior commissure is a scattered structure in *Scyllium* and that the stria terminalis as a distinctive structure is not observable therein, though it is probably represented by some few fibres, as also is the poorly developed "fornix" system. The characteristic line of olfactory discharge is ostensibly through the habenular system. There may also be a small efferent system in the tractus pallii itself, but of this nothing certain is known. At any rate it must be clearly understood that these efferent paths adjacent to the pallial tract (amygdaloid) cortex only secondarily enter into the constitution of the so-called amygdaloid complex. The nucleus of the diagonal band of Broca (when distinct from the tuberculum olfactorium) and the nucleus taeniae (site of origin of the tractus taeniae) are definite cortical areas.

In Selachians the site of origin of the tractus taeniae (somatic area of Johnston) is so clearly cortical as to have misled Johnston. It covers the palaeostriatum. Throughout phylogenesis this relationship of the nucleus

of the tractus taeniae is preserved. Fig. 15 illustrates that this is true for *Sphenodon* and this "Rindenabtheil" of the amygdaloid complex of Völsch is the area which in the turtle Johnston has failed to distinguish from his "large-celled medial nucleus." The habenular tract arising in this nucleus (a true cortex in Selachians) overlying the palaeostriatum is to be regarded probably as the most primitive efferent path through the habenula. When a true olfactory cortex in the shape of a pyriform and a nucleus of the lateral olfactory tract appeared lateral to the palaeostriatum, its posterior efferent fibres utilised the path laid down by the tractus taeniae. These areas lying adjacent to one another and subserving similar functions are to be recognised in the Reptilia but not as clearly as in Selachians. In the Reptilia too, the problem is complicated by the fact that many of these efferent fibres utilise the more direct path to the hypothalamic region, omitting the synapse in the habenula. They appear to have found the path to the hypothalamus along the line of the tractus pallii which they accompany and would undoubtedly utilise the path of the efferent portion of this tract if such exists. This would explain how the more primitive habenular efferent system characteristic of Selachians may give rise to the taenia semicircularis and stria terminalis systems which are found from the Reptilia onwards.

What natural tendency there is for these similarly-functioning areas to come closer together is heightened in the Reptilia by two factors; first, actual stretching of their axones in the so-called "olfactory projection tract of Cajal" to form the characteristic taenia semicircularis; and second, the expansion of the cortex represented now by a definitely developed hippocampal formation, a true pyriform and a nucleus of the olfactory tract, a huge parahippocampal cortex and lastly the primordium neopallii.

The net result of all these factors of a mechanical nature and undoubtedly also active neurobiotactic influence is to heap the primitive palaeostriatal cortex into a nuclear mass: but even in the specialised mammalian classes it will be recollected that Cajal found fibres arising from that region called by him "cortical part of the amygdala". An examination of his text and figures (*op. cit.*) shows that this region corresponds with that termed subiculum hippocampi by Drs Winkler and Potter. It is indeed continuous in Mammalia (owing to the "extrusion" of the "nucleus amygdalae proprius" from its ventricular position as the nucleus tracti pallii in the Selachian forebrain) with the subiculum on the medial aspect and the pyriform laterally. This region discharging into the same areas as the posterior part of the pyriform lobe and lateral olfactory tract is homologous with the nucleus tracti taeniae. Like that region—so clearly differentiated in Dipnoi and other fishes—it is continuous anteriorly with the cortex of the tuberculum olfactorium and nucleus of the diagonal band of Broca, and is the relic of probably the most primitive lines of discharge of correlated olfactory impulses through the habenula, and in higher forms through the hypothalamus also. It may be regarded as the most posterior portion of the "palaeostriatal cortex."

The work of Völsch has shown that this mass is a "Rindenabtheil." This area he has copiously described and figured and we can unhesitatingly regard it as the structure termed the "subiculum cornu Ammonis" by Drs Winkler and Potter, the element *B* of both this paper and that of Völsch, or what may be far better designated as the "palaeostriatal element" of the amygdaloid complex.

That this association of fundamentally differing parts has not been clearly conceived is shown by the fact that it is dealt with "en bloc" by certain writers (e.g. Kappers, '08, in stating that the "secondary epistriatum which is closely related with the tertiary smell-cortex comes to take a wholly caudal and basal situation as the nucleus amygdalae"). This "secondary epistriatum" of birds is probably a far more highly differentiated area than, but is entirely homologous with, the "hypopallium posterius" of this article. Its relationships are most distinct, and will receive immediate attention.

THE ELEMENT *C*

There is a conspicuous element in this morphologically posterior part of the forebrain which, as far as my knowledge goes, has either been unrecognised or wrongly interpreted by previous investigators. If horizontal sections of the brain of *Scyllium* (fig. 11) be examined in series it will be discovered that in a region, corresponding in situation with the hypopallial rudiment posteriorly, a tract takes origin. It is difficult to distinguish in specimens prepared by the method of Weigert exactly where the posterior limit of the afferent tracts to, and the anterior limit of the efferent tracts from, this longitudinally differentiating hypopallial rudiment, are to be set. In short the most anterior region is mainly an afferent nucleus while the posterior is mainly efferent. In *Scyllium* this posterior efferent part of the hypopallium gives rise to fibres which become bunched together forming the most medial fibre constituent of the region. It later meets the other efferent tracts with which it ascends to the habenula. It appears to be the main discharge mechanism for the newly differentiating hypopallial region.

Sphenodon provides us with a remarkable confirmation of this tentative explanation. The hypopallium in *Sphenodon* has a very definite double constitution for while the anterior part is solid in cell formation the posterior part has a scattered arrangement—a thing which is most conspicuous in longitudinal sections. Here we find also (figs. 17 and 17 *a*) that there has been a crumpling at the line of differentiation between the two portions of hypopallium. The study of the fibre tracts shows that while the anterior portion (figs. 17 and 17 *a*) is the goal of the afferent system from the thalamus, the posterior region discharges by a tract which runs at any rate for the most part to the habenula. It may also discharge in part to the hypothalamus in Reptilia. This hypopallio-habenular constituent, then, is clearly marked in fishes and in reptiles, and evidently must have its homologue in Mammalia.

The habenula gradually decreases in relative importance in phylogenesis and as has been pointed out an increasingly large portion of the efferent system utilises the more convenient passage through the hypothalamic region.

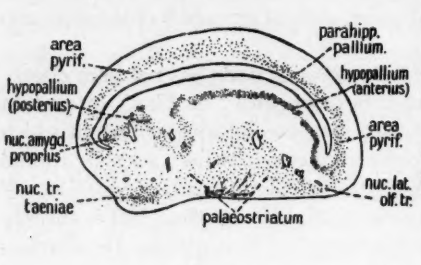


Fig. 17.

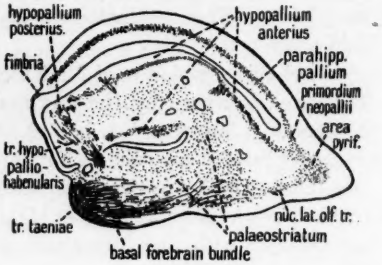


Fig. 17 *a*.

In the diagram reproduced (fig. 16) from the work of Winkler and Potter I have not discussed that element of the amygdaloid complex termed by them the "nucleus amygdalae." From what has been written it is clear that this portion of the complex corresponds in every detail with that posterior region of the hypopallium which discharges (in Selachii and Reptilia) through the habenula for the main part. It only becomes related secondarily to that portion of the palaeostriatal cortex which we have identified as the nucleus tracti taeniae and is very distinct in Selachians, being continuous with the hypopallial bulging into the ventricle. It has apparently been compressed during phylogeny owing to the mechanical changes affecting the expanding cortex and corpus striatum but must be recognised as originally a hypopallial and not a palaeostriatal constituent. It has therefore been designated as such in fig. 18, taken from the *Notoryctes* series, somewhat anterior to fig. 13.

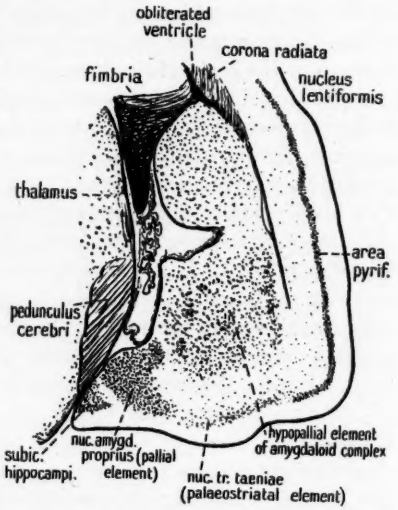


Fig. 18. Ventral half of transverse section of brain of *Notoryctes* some sections anterior to that represented in fig. 13 of this paper. Note the relationships of the three elements of the amygdaloid complex.

In his painstaking monograph Völsch has closely observed this region: "the nucleus amygdalae of Ganser," which he himself has termed the "Areas *M* and *T*." He has shown how in certain classes of Mammalia this mass in

ontogeny is forced away from its ventricular position "by the development of the stria and the corpus striatum," and further, that its identity is rendered distinct by a kind of capsular formation, presumably of fibrils. Such a separate element of the amygdaloid complex is certainly the "nucleus amygdalae of Winkler and Potter," which has been regarded (as Völsch has shown) by some as portion of the lentiform nucleus, but by cytological structure and fibre connections it is an element of the amygdaloid complex. It is as clearly too the homologue of the hypopallium posterius (mihi) in Reptilia and forms the element *C* or more suitably the "hypopallial element" of the amygdaloid complex.

It is not part of my scheme here to criticise the work of Völsch. That it shows obvious fallacies has been recently exposed by Landau ('19) and as Elliot Smith has himself shown ('19) the claustrum is cortical; and so the views of Meynert ('67) to-day find confirmation. He (Völsch) thinks that the amygdaloid complex arises by a "sinking in" of what he has called the "intermediate area" of the pyriform lobe, and insists on the corroborative evidence of the two sulci to be found in this region. Such a view would rather naturally follow (see figs. 13 and 18) from researches which, as I have already stated, are confined to the Mammalia. It was the recognition of this that drove me from the study of *Notoryctes* to that of *Scyllium*. The phylogenetic history of this site of early transformations is to be sought in the lowliest and not the more highly organised Vertebrata. His insistence upon the finer cytology of the three constituent elements of the complex which he himself has discovered to be fundamental may have some justification when we are more fully acquainted with the causal factors in the production of its more intimate fibre connections. In the solution of this problem, the Reptilia may afford valuable evidence: for the hypopallium anterius of Reptilia is not a uniform structure. It shows a degree of differentiation which it should be possible to correlate with the different types of stimulus reaching it from the thalamus and it is to be expected that the hypopallium posterius is correspondingly complex. Here lies the key not only to the proper appreciation of the differentiation of cell structure within the three groups found in the mammalian amygdaloid complex by Max Völsch, but also to the understanding of the curious development of the striatal regions in Aves.

It must further be remembered that in the amygdaloid region deep to the "Rindenabtheil" (cortical part of the palaeostriatum) there are scattered cells of the palaeostriatum itself filling up the space between the three elements but not obscuring their identity.

A RETROSPECT
(the terms basal and cortical)

For the last quarter of a century and more, the attention of morphologists has been directed to the elucidation of the so-called basal regions of the forebrain. Nothing has done more towards a correct evaluation of the components in this district than the researches of Elliot Smith upon the nature of the

"paraterminal body" and "commissure bed," which cleared the way for the appreciation of the hippocampus throughout the vertebrate series. His differentiation between a rhinencephalon and neopallium has been an illuminating conception for the whole of neurological phylogeny. But within the rhinencephalon itself there had been transformations of an exceedingly intricate character long before a neopallium emerged. And these were the changes concerned in the evolution firstly of the palaeostriatum and later of the hypopallium. What was the character of those impulses that first impinged upon the original simple olfactory reception centre, which later grew to be the dominant mechanism of the body, is difficult to say with certainty. They were probably imperfectly differentiated impressions coming up from the massively-responding thalamus of the primitive vertebrate. These newly entering impulses stimulated cell formation in the deeper part of the primitive cortex. The cells by neurobiotactic influence naturally tended to aggregate in the ventral and juxta-thalamic region, while the dorsum of the primitive vesicle remaining freer from disturbing influences became the seat of the formation of a true pallium (cortex).

The nature of the disturbances in a primitive olfactory mechanism caused by this early entrant tract is well illustrated in a diagram (fig. 19) taken from Kappers (*Anat. Anz.* Bd. XXXIII. 1908): but in that figure the more salient example of his neurobiotactic principle is exemplified, not by those cells migrating towards the source of stimulus in the olfactory bulb, but rather by those heaped up round the newly entering tract from below. Such a degenerate Amphibian forebrain shows practically no palaeostriatal differentiation, but in the more clearly differentiated brain of the Selachian the pallium in the region of the palaeostriatum is represented by a cortical formation which rapidly became variously modified for particular purposes. The process of differentiation of this "palaeostriatal cortex" has advanced to the degree recognised in its various elements as we know them, though all the steps in their history are still far from clear. It is probably, broadly-speaking, true that the tuberculum olfactorium proper is a receptive centre for olfactory impulses, that the diagonal tract of Broca is a correlation mechanism between the various olfactory cortices and that the tractus taeniae is an olfactory efferent tract, but there is just as probably much more. The Selachian forebrain also shows us how these earlier cortices developed out of an apparently homogeneous formation lying over the palaeostriatum. But it shows us more, for already we discover an additional disturbing element in the mechanism

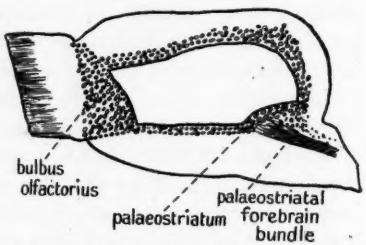


Fig. 19. Taken from Kappers (*op. cit.* '08) to illustrate the possible nature of the conditions arising by the entry of the first "thalamic" impulses leading to the differentiation of a palaeostriatum in the primitive olfactory receptor. Sagittal section of forebrain of *Axolotl*.

which we are now in a position to term a forebrain. It is the only ascending tract we know from the hypothalamus; and in Selachians it has reached a portion of the primitive pallium by a course through, and lateral to, the optic chiasma. It is the tractus pallii the relationships of which have already been discussed. It is possibly the bearer of impulses interpreted by this primitive forebrain as taste and it has its homologue throughout the vertebrate series as the "nucleus amygdalae proprius."

But by far the most significant event in the history of the vertebrate phylum is the entrance for the first time into the forebrain of the Selachian of that dorsal thalamic and presumably also tectal group of fibres, which, passing through the palaeostriatum, invade the pallial formation beyond it and lead to its differentiation into two definite regions, which we have recognised as the hypopallium and nucleus of the lateral olfactory tract respectively. Concerning the impulses borne by this fibre tract we are still ignorant, but it is probable that they are concerned with some degree of tactual discrimination, and the coarser appreciation of sight and sound. And significant is the fact that, together with the changes accompanying the entrance of this tract, there is a specialisation for the discharge by a particular path of the correlated response. This is conceivably by way of the tract here described as the hypopallio-habenular and its homologues.

The origin of the neopallial primordium is a further advance which affects the anterior portion of the hypopallium. It is apparently foreshadowed in the Selachian but it is very clearly present in reptiles, as has been shown by Crosby, Elliot Smith, and Woollard (in a paper read before the Cambridge meeting of the Anatomical Society), and, as I have personally observed, even in the archaic *Sphenodon*. It is a striking fact that these successive modifications of the original olfactory mechanism have affected successively more and more anteriorly lying portions of the forebrain, and that then, the expansion of the region invaded has led to large alterations in shape and relationship of the various areas.

It is clear from these remarks that the usage of the terms "basal" and "cortical" will need definition if they are to remain intelligible expressions of neurological terminology.

Throughout the whole vertebrate series known to us there is no such thing as a pure rhinencephalon; in that primitive vertebrate which possessed a palaeostriatum only, this structure was an addition, a well-defined correlation mechanism composed of gross afferent and efferent elements. Even some term such as "archipallium" which was introduced by Edinger is quite inadequate without definition. There are four definite stages (and perhaps five—if we regard the entrance of the tractus pallii as a stage) in the development of the forebrain—an original olfactory receptor, or placodal stage, a palaeostriatal stage, a pallial stage, a hypopallial stage and a neopallial stage, and the terminology of the forebrain can only be rational when based upon this wide phylogenetic survey.

REFERENCES

Beccari, Nello. "Le sostanza perforate anteriore e i suoi rapporti col rinencephalo nel cervello dell' uomo." *Archivo di Anat. e di Embriol.* vol. x. 1911.

Cajal, S. Ramon y. *Histologie du Système Nerveux.* Paris, 2 vols. (translated from the Spanish by Dr L. Azoulay), 1909–11.

Crosby, Elizabeth C. "The Forebrain of *Alligator mississippiensis.*" *Journ. Comp. Neurol.* 1917.

Gisi, Julia. *Inaugural Dissertation zur Erlangung der Doctorwürde Universität.* Basel, 1907.

Herrick, C. Judson. "On the Centers for Taste and Touch in the Medulla Oblongata." *Journ. Comp. Neurol. and Psych.* 1906.

—— "On the Phylogenetic Differentiation of the Organs of Taste." *Journ. Comp. Neurol. and Psych.* 1908.

—— "Morphology of the Forebrain in Amphibia and Reptilia." *Journ. Comp. Neurol.* 1910.

—— "Midbrain and Thalamus of Necturus." *Journ. Comp. Neurol.* 1917.

Johnston, J. B. "The Brain of Petromyzon." *Journ. Comp. Neurol.* 1902.

—— "Morphology of Forebrain Vesicle in Vertebrates." *Journ. Comp. Neurol.* 1909.

—— "The Evolution of the Cerebral Cortex." *Anat. Record,* 1910.

—— "Telencephalon of Selachians." *Journ. Comp. Neurol.* 1911.

—— "Morphology of the Septum, Hippocampus and the Pallial Commissures in Reptiles and Mammals." *Journ. Comp. Neurol.* 1913.

—— "The Cell Masses in the Forebrain of the Turtle." *Journ. Comp. Neurol.* 1915.

Kappers, C. V. Ariens. "Die Phylogenese des Corpus Striatum und der Vorderhirn-Commissuren." *Folia Neurobiologica,* 1908.

—— "Weitere Mittheilungen über die Phylogenese des Corpus Striatum und des Thalamus." *Anat. Anzeiger,* Bd. xxxiii. 1908.

—— "Die Phylogenese der Paläeocortex und der Archicortex vergleichen mit der progressiven Entwickelung der Sehrinde. *Deutsch. Zeitschrift für Nervenheilkunde.*" Bd. xxxvi. 1908.

Kappers and Theunissen. "Zur vergleichenden Anatomie des Vorderhirns der Vertebraten." *Anat. Anzeiger,* Bd. xxx. 1907.

Kappers and F. W. Carpenter. "Das Gehirn von Chimaera monstrosa." *Folia Neurobiologica,* 1908.

Landau, E. "The Comparative Anatomy of the Nucleus Amygdalae, the Claustrum and the Insular Cortex." *Journ. of Anat.* (together with a note on Prof. Landau's Memoir by G. Elliot Smith), 1919.

Lange, S. J. de. "Das Vorderhirn der Reptilien." *Folia Neurobiol.* 1911.

—— "L'évolution phylogénétique du corps strié." *Le Nevraxe,* vol. xiv. 1913.

—— "Das Zwischenhirn und das Mittelhirn der Reptilien." *Folia Neurobiol.* Bd. vii. 1913.

Sheldon, R. E. "The Olfactory Tracts and Centers in Teleosts." *Journ. Comp. Neurol.* 1912.

Smith, G. Elliot. Catalogue of Physiol. Series of Comp. Anat. Museum of Royal Coll. of Surgeons of England, vol. ii. 2nd edition, 1902.

—— "The Cerebral Cortex in Lepidosiren." *Anat. Anzeiger,* Bd. xxxiii. 1908.

—— "The Arris and Gale Lectures." *The Lancet,* Jan. 1, 15 and 22, 1910.

—— *The Central Nervous System in Cunningham's Anatomy,* 3rd edition, 1913.

—— "A Preliminary Note on the Morphology of the Corpus Striatum and the Origin of the Hypopallium." *Journ. of Anat.* vol. liii. 1919.

Thomson, J. Stuart. "Morphology of Prosencephalon of Spinax, etc." *Trans. Roy. Soc. of Edin.* vol. lii. Part ii. 1918–19.

Tretjakoff, D. "Brain of Ammocoetes." *Archiv für Mikr. Anat. und Entwick.* Bd. lxxiv.

Völsch. "Anatomie des Mandelkerns, etc." *Archiv für Mikr. Anat.* 1906.

—— "Zur vergleichenden Anatomie des Mandelkerns, etc." *Archiv für Mikr. Anat.* 1910–11.

THE BASAL ARTERIES OF THE FOREBRAIN AND THEIR FUNCTIONAL SIGNIFICANCE

By JOSEPH L. SHELLSHEAR,

Demonstrator of Anatomy, St Bartholomew's Hospital, London

The recent important investigations of Professor Elliot Smith in reference to the phylogenesis of the corpus striatum, and more especially to the particular significance which he has attached in that paper (1919) to the vessel which he has termed the lateral striate artery in Reptiles, has made it obvious that a more searching investigation than has hitherto been made into the nature of the blood vascular supply of the so-called basal regions of the cerebral hemispheres might supply corroborative evidence in the elucidation of these morphological problems.

At his suggestion I undertook this investigation in the Anatomical Department of St Bartholomew's Hospital.

The research has not only justified these anticipations, but in addition has revealed some important discrepancies in the work of previous investigators in this field.

But further, when viewed in the light of Stopford's contribution to the study of the "Blood Supply of the Pons and Medulla," it has strongly confirmed the opinion of Hilton that the arteries of the body are laid down with remarkable precision, and that their distribution is closely associated with the function of the part supplied. For these reasons I have felt, that, despite the incomplete nature of the data in my hands, a record should be made of the results obtained to serve as a stimulus to further investigation, since circumstances have rendered it impossible for me to carry this work to a more complete stage at the present time.

TECHNIQUE

The methods employed in this work are the same as those used by Beevor (1909) except that it was found more convenient to use a record syringe instead of Beevor's pressure apparatus to inject the basal vessels.

THE ARTERIAL SUPPLY OF THE CLAUSTRUM

In his paper, previously referred to, Elliot Smith suggests that the claustrum is represented in Reptiles by the hypopallium, where it turns in from the pyriform area. Now if the arterial blood supply is to be of any value as a phylogenetic criterion, then the claustrum should be supplied by the lateral striate group of arteries, unless perchance John Hunter's view is

correct that "the course of the arteries is such as will convey the blood most conveniently.... whoever, therefore, discovers a new artery, vein, or lymphatic, adds little to the stock of physiological knowledge."

Dealing with the actual question of the arterial supply of the claustrum. In his investigation of the blood supply of the brain Duret realised the phylogenetic importance of the vessels and made use of his findings in an attempt to confirm the then existing views on the origin of the claustrum.

He states: "The claustrum receives some fine arterioles which penetrate the convolutions of the Island of Reil. It is supplied exclusively by these vessels and ought not to be included in the circulation of the corpus striatum. One knows moreover that this grey band is only a detached portion of the grey matter of the neighbouring convolutions. We have never seen any anastomosis between these arteries and those of the corpus striatum." Beevor (1909) confirms the findings of Duret, stating that: "The claustrum and external capsule are supplied by the cortical arteries which penetrate from the insula and that there is no connection between the arteries to these structures and those of the adjoining lenticular nucleus."

The observation of both these investigators, that no anastomosis occurs between the vessels to the claustrum and those to the lenticular nucleus, is a very important one, as we shall see shortly, and it is interesting in that it confirms the opinion of John Hunter (the first to describe end arteries) that the arteries entering the brain substance do not anastomose with one another. My own work also confirms this observation. In contrast with Duret's statement, however, I would point out that, in his illustration here reproduced (fig. 1), he shows the claustrum as being supplied in part by branches of the lateral striate artery.

Unfortunately Beevor's specimens, showing his injections of the claustral region, are not accessible, but a careful study of his memoir and of his beautiful specimens in the Museum of the Royal College of Surgeons, has impressed me with the accuracy and value of his work.

I was surprised therefore to find, when I injected the middle cerebral artery at its origin and clamped off the vessels to the insular cortex, that the claustrum was clearly injected together with the lenticular nucleus, whilst the insular cortex was not injected. This I repeated in three other cases with the same result.

In my cases there is no communication between the vessels of the insular cortex and those of the claustrum.

In the cases described by Beevor and Duret there is no communication between the vessels of the lenticular nucleus and those of the claustrum.

The discrepancy in the two results is explained by the fact that on examination of my specimens one sees a separate and distinct series of fine vessels passing through the limen insulae to reach the claustrum. These are basal branches of the middle cerebral, arising more laterally than the commonly named lateral striate arteries.

The ligatures applied by Duret and Beevor must have been placed on the medial side of this series of vessels, and they had presumably regarded any vessels arising lateral to the lateral striate as cortical. This view is at once true and false: phylogenetically the claustrum is cortical, but as it is a definite part of the corpus striatum, from the point of view of blood vascular relationship, it may be considered quite as definitely basal.

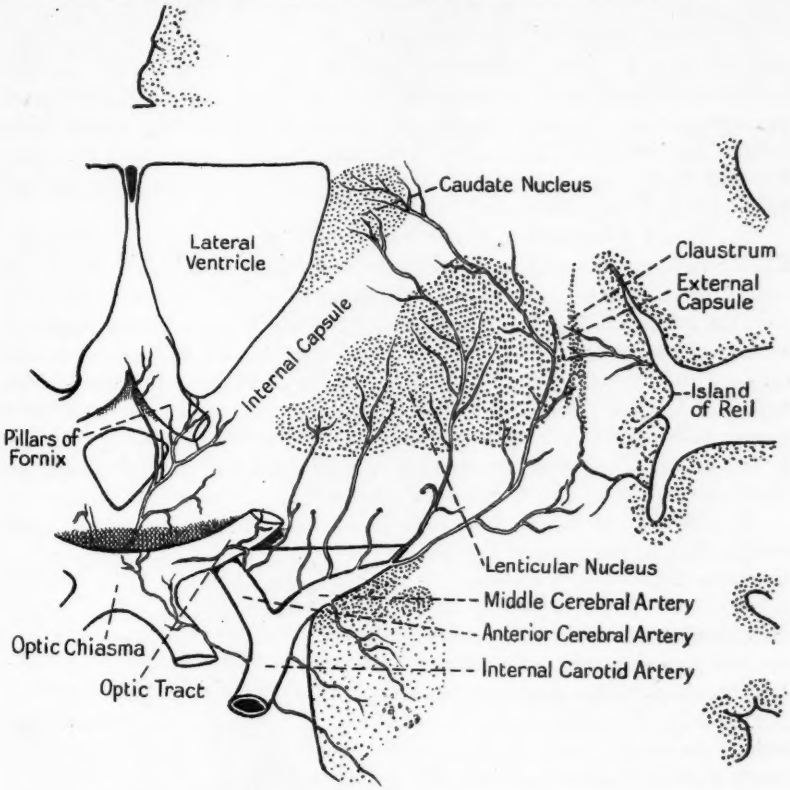


Fig. 1

In order to demonstrate this series of vessels I placed a cannula in the middle cerebral artery at its origin and applied a ligature medial to the claustral arteries. I next placed a cannula distal to the claustral arteries but proximal to those of the insular cortex. I then injected the proximal segment of the middle cerebral in red and the distal segment in blue, with the result that the insular cortex was unstained, the claustrum stood out as a blue crescent and the portion of the lenticular nucleus injected stood out in red.

Unfortunately this specimen was not ready when this paper was read before the Society. It is however to be seen in the Museum of the Royal

College of Surgeons, where it provides a vivid demonstration of the discrete character of the blood supply to all three parts.

It is thus perfectly clear that the claustral arteries are not branches of the lateral striate, but arise as a special group in series, on the one hand with the cortical vessels of the island, and on the other hand with those arteries which have been identified as the special arteries of cerebral haemorrhage by Charcot.

In this connection it is interesting to relate the following statement by Charcot (1881): "The Thalami together with the Corpora Striata are the most common seats of haemorrhage; and yet certain authors have announced the opinion that in the majority of cases the haemorrhage takes place outside the corpus striatum. This is an exaggeration rather than an error, for next to the opto-striate bodies the spot most frequently attacked by haemorrhage is the claustrum."

The recent contribution to the morphology of the corpus striatum by Elliot Smith, and the still more recent paper by Dart in this Journal on the same subject, seem to give peculiar significance to the fact already emphasized that the arteries in this region are end-arteries and in series with the cortical arteries of the insular cortex. Elliot Smith has explained the appearance and origin of the hypopallium as an infolding of the cortex and Dart has shown that the folding follows the differentiation of the deeper layer of that cortex whose superficial layer is the nucleus of the lateral olfactory nucleus in Selachians. These changes have taken place lateral to the palaeostriatum which is covered by the tuberculum olfactorium.

If this differentiation and increase of the nature of a hypertrophy occurs, then in the place of a primitive even distribution of cortical end-arteries, one would expect to find an enlargement of the end-arteries at the place where hypertrophy has occurred. This occurs at the site immediately lateral to the palaeostriatal region (as was phylogenetically deduced by Elliot Smith) and not from the insular cortex. It must however be recognised that the artery which he termed lateral striate in Reptiles is not the lateral striate of human anatomy. The lateral striate of human anatomy, as Charcot pointed out, passes into the lentiform nucleus and is probably palaeostriatal, because it is much more medial in position than the claustral (or hypopallial) arteries, which I consider correspond with the lateral striate in Reptiles. I have therefore named these vessels accordingly in fig. 2.

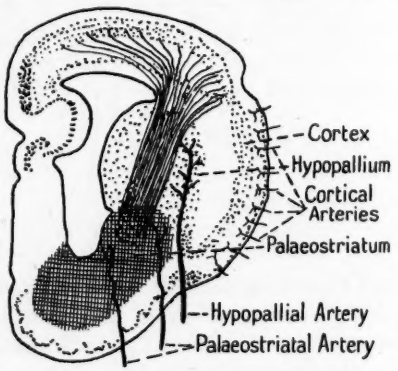


Fig. 2

There is little necessity to stress further than Charcot has done the clinical significance of such large cortical end-arteries as we have here represented.

THE DISTRIBUTION OF THE VESSELS IN RELATION TO THE ANTERIOR PERFORATED SPOT

The usual descriptions and illustrations given in text-books of these vessels have become so diagrammatic from continual repetition that it is difficult to reconcile what is actually found with the descriptions given.

Figs. 3 *A*, *B* and *C* show the appearance of three typical specimens of the anterior perforated spot.

A row of perforations lies in close relation to the endorhinal fissure placed postero-internal to the lateral olfactory stria.

Except at the lateral angle of the space, where there are bunched together five or six perforations larger than the remainder, these perforations are arranged in a row roughly in two series.

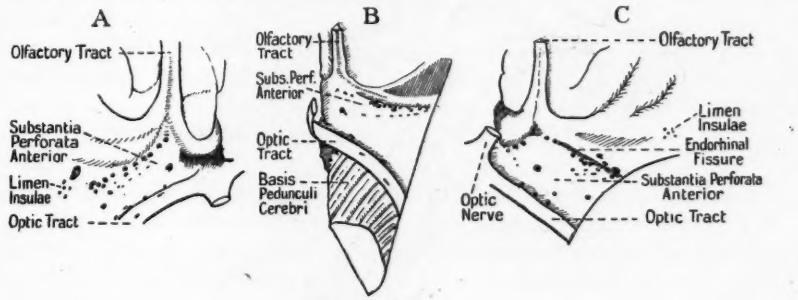


Fig. 3

Laterally to these perforations can be seen the fine perforations on the limen insulae caused by the claustral arteries.

The perforations in relation to the olfactory stria average from 18 to 20 in number.

The usual description of these basal arteries is as follows: the anterior cerebral artery gives off antero-mesial basal branches which pierce the inner part of the anterior perforated spot and the lamina terminalis. The middle cerebral supplies antero-lateral basal branches perforating the anterior perforated spot. These antero-lateral branches are further divided into mesial and lateral striate arteries.

To correspond therefore with the perforations the antero-lateral branches of the middle cerebral artery should be approximately 18 in number. An examination however of an injected brain, sectioned horizontally just above the anterior perforated spot, shows that of the 18 openings the outer 5 are middle cerebral, and of the remainder only 4 or 5 are middle cerebral, the others being anterior cerebral branches.

Of the two rows of openings the anterior is occupied by the anterior cerebral branches, the posterior by the middle cerebral.

It is very interesting to observe that a section through the anterior commissure in this specimen shows that, at this level, the corpus striatum in front of the commissure, together with the commissure itself, is supplied by the anterior cerebral artery, the area lateral and postero-lateral by the middle cerebral. Finally the area postero-mesial to it is supplied from without inwards by the anterior choroidal, the posterior communicating and the posterior cerebral arteries. Thus the anterior commissure is the dividing line between five different arteries, and this I have confirmed in one of Beevor's specimens.

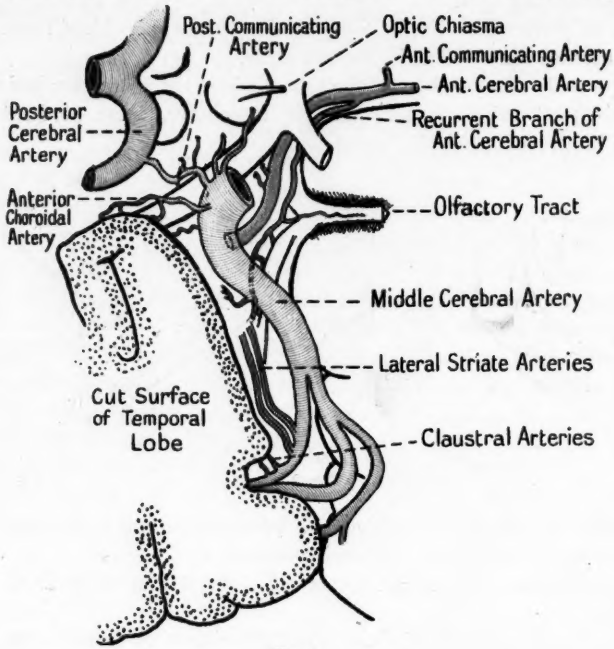


Fig. 4

When one considers with this fact the complicated phylogenetic changes which have taken place round this area, it seems clear that arteries are laid down in no haphazard fashion.

A reference to fig. 4 explains the supply of the anterior cerebral artery, and also impresses the necessity for a revision of the nomenclature of these vessels. The anterior cerebral gives off, in all the specimens I have examined, a recurrent vessel in the neighbourhood of the anterior communicating artery, and in one case distal to it. This vessel passes backwards and outwards to the lateral angle of the space, and there enters the brain substance closely related to the lateral striate group of the middle cerebral.

Contrary to Duret's observations, and in confirmation of Beevor's, I have been unable to find any supply to the optic thalamus from the lateral striate arteries, and consider that the name lenticulo-optic artery should be omitted from anatomical nomenclature.

It is of interest here to observe the angles at which these vessels come off from the anterior and middle cerebral arteries. Text-book illustrations show them as a neatly arranged row coming off at right angles, whereas I have noticed that the larger the vessel entering the substance of the brain, the more acute is the angle it makes against the direction of the current; and to attain this end both sets from the anterior and middle cerebral leave the parent trunk at a considerable distance from the place of entry into the anterior perforated spot. It is strange that no reference to this fact, which must have an important clinical bearing, can be found in the literature, except in *John Hunter's Works*, p. 220. He states:

"I have already observed that the angles at which the branches of an artery arise may either retard or allow a freer motion of the blood; but nature appears to have taken still more care in retarding the blood's motion when velocity might do mischief. She seems also to have taken more care about the blood's motion in some parts than in others; as for example, in the brain, a part which probably cannot bear the same irregularity, in quantity or velocity of the blood, as many other parts of the body."

Directly posterior to the division of the olfactory tract, and lying immediately in front of the optic tract, is a well marked perforation into which passes a branch of the anterior cerebral artery. In the specimen from which fig. 3 *B* was taken there was a line of very fine perforations leading from this perforation to the lateral angle of the space. Except for this opening the only other perforations are of insignificant size.

The precise nature of the distribution of the anterior and middle cerebral arteries is also to be found in the other vessels of the brain.

Thus I find that the posterior cerebral and posterior communicating arteries are so precisely distributed in my specimens that the description given by Beevor of the arterial supply of the optic thalamus could well have been made from my specimens.

I would refer my readers to his paper for a more detailed description of the blood supply of this structure. It is sufficient here to say that the anterior nucleus is supplied by the posterior cerebral, and the injected nucleus stands out as an island in the rest of this part of the thalamus; and roughly speaking, that, of the remainder of the thalamus, the anterior portion is supplied by the posterior communicating, and the posterior portion, including the pulvinar and the external geniculate body, is supplied by the posterior cerebral artery.

A reference to Sachs's investigations on the function of the thalamus in *Macacus*, reveals the fact that the subdivision of the thalamus into functional areas by him very closely coincides with the areas of blood vascular distribution as found by Beevor and myself.

Thus he found that the anterior nucleus was extremely unexcitable to electrical stimulation, and further we know that into this nucleus passes the fasciculus mammillo-thalamicus, and there is reason to associate this nucleus with the sense of smell.

Similarly the distribution of the other basal branches of the posterior cerebral is closely associated with vision.

That this association between blood vascular distribution and function, so suggestive in the thalamus, is no mere coincidence, is clear from the complete and exact account of the blood supply of the pons and medulla oblongata by Stopford and from the distribution of the blood vessels in other parts of the body in their relation to function first clearly demonstrated by John Hilton.

Stopford's clear-cut areas in the medulla oblongata demarcating the hypoglossal nucleus in the case of the anterior spinal artery, the trigonum vagi in the case of the vertebral artery, and the trigeminal nucleus in the case of the posterior inferior cerebellar artery, are so similar in type to the areas of the corpus striatum shown by me, and the optic thalamus by Beevor, that we are justified in using the blood supply as confirmatory evidence in investigation of function.

Furthermore, when one considers the ingenious experiments on brain function by such investigators as Sherrington, it seems to be within the range of practical experimentation to determine function by cutting off the blood supply to known areas.

The morphological and functional importance of the distribution of arteries receives a further significance from Blackburn's report on the abnormal median anterior cerebral artery, as found among the insane. He finds that this abnormality is much more frequent among the insane, and states that the frequent variations of this system of vessels suggest instability of ontogeny and phylogeny.

It seems possible to enunciate the two following principles:

(1) That arteries are laid down with a definite relation to function.

(2) That the distribution of arteries obeys some definite ontogenetic and phylogenetic law.

This problem, which was before me throughout, viz., the relation of blood supply to function, is far from its full explanation, and yet there is one aspect of it which deserves special consideration, as it arises directly from the material provided by this investigation. There is a free capillary anastomosis between the cortical and hypopallial arteries on the one hand, and the hypopallial and palaeostriatal arteries on the other hand, and yet no opening up of this capillary network to form connecting arterial channels takes place.

Such an arrangement provides us with a critical problem in the question of the relationship of arterial supply to function, for we are now in such a position of precise knowledge as to the origin of the claustrum that the fact of the preservation of the original reptilian type of blood supply, throughout the mammalian series (as shown in fig. 2), illustrates that arteries once

laid down, maintain their anatomical and presumably functional integrity throughout phylogeny.

The only hypothesis which I can suggest to explain this precision of distribution is the following: In an evolutionary sense it must be to the advantage of the organism that the blood supply to a part or parts of its structure concerned with some special function should be capable of being adjusted to its requirements at any given time.

Such a co-ordinating and accommodating mechanism for the blood supply is found in the vasomotor system. When a particular area, such as the hypopallium, develops and differentiates, its vascular supply, although more elaborate, remains under the influence of the same controlling apparatus.

Perhaps no more beautiful illustration of this could be found than in the blood supply of the palate.

Hilton says: "Curiously enough, this soft palate receives six arteries, three on each side: one from the facial, one from the ascending pharyngeal and one from the internal maxillary, the true 'masticatory artery.'

Here then is a simple piece of anatomy, which shows the precision and purpose of the distribution of arteries which seem to be associated with three different important functions: one in relation to respiration, the facial artery; another in relation to deglutition, the ascending pharyngeal artery; and a third in relation to mastication receiving its supply from the masticatory artery."

In conclusion I wish to express my thanks to Dr Macphail of St Bartholomew's Hospital for his assistance in this work, to Mr R. Keene for the drawings he has made for me, and to the Pathological department of the same institution for the supply of material used in this investigation.

REFERENCES

Elliot Smith. *Journal of Anatomy*, vol. liii. 1919.
Stopford. *Journal of Anatomy*, vol. l. pt iii. 1916.
Beevor. *Phil. Trans. Roy. Soc.* vol. cc. 1909.
Duret. *Arch. de Physiol.* 1873 and 1874.
Charcot. *Lectures on Senile Diseases*, 1881.
John Hunter. *The Works of John Hunter*, vol. iii.
Sachs. *Brain*, Part cxxvi. 1909.
Blackburn. *Journ. of Comp. Neur. and Psych.*
John Hilton. *Rest and Pain*, 1880.

FUSION-LINES OF BONES

By ZACHARY COPE

In a previous communication on the internal structure of the sphenoidal sinus I stated that there is evidence to show that the bone formed at the line of fusion of bony centres may be and often is of a denser and more resistant material than the tissue on either side of the line.

Though I believe evidence to support this statement must be known to all those who have made a study of the internal structure of the long bones yet I have thought it an interesting investigation to see in what parts of the skeleton such fusion-lines can be recognised and at what age they become indistinguishable from the neighbouring bone.

For this purpose I have examined sections of fully-developed dried bones and radiograms of fully-grown individuals of different ages. The conclusions arrived at, and illustrated by the accompanying radiograms and photographs, are as follows:

The lines of fusion between the epiphyses and diaphyses of the long bones can be recognised in many cases until a late period of life. The fusion-line persists as a somewhat irregular line of thin compact tissue, or as a narrow belt of cancellous tissue denser than the bone on either side. The lines are best seen and most persistent in the bones of the lower extremity where the stress is greatest. The junction of the great trochanter and the head of the femur with the diaphysis are usually distinct years after the bone is fully grown (fig. 1). The most remarkable persistence is seen at the site of the epiphyseal lines at the lower end of the femur and the upper end of the tibia, for a thin but dense line of bone can be seen in these situations in patients who are sixty and even seventy years of age (figs. 2, 3, 4). Radiograms show this line fairly constantly and one would be likely to take the bone as that of a much younger person unless aware of the fact of persistence of the fusion-line (fig. 5). The lines at the lower end of the tibia and fibula persist for some years but not so definitely.

In the upper extremity the fusion-lines are not so persistent. At the upper end of the humerus the position of fusion between the head and shaft (morphological neck) can usually be distinguished in a fully ossified bone as two denser lines of bone enclosing an obtuse angle between them. At the lower end of the humerus a transverse fusion line may be seen frequently, but the bones of the forearm seldom show very definite indication of such a line.

The metacarpal and metatarsal bones and the phalanges not uncommonly show some, though seldom very definite, evidence of denser bone at the epiphyseal junction-line.

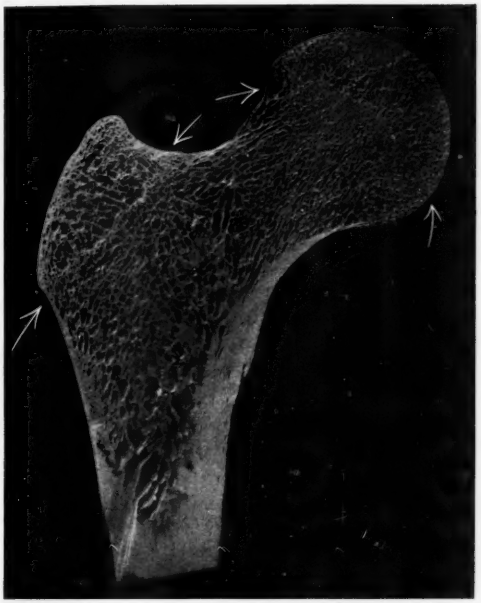


Fig. 1. Section of upper end of femur from a full grown adult (R.C.S. Museum).

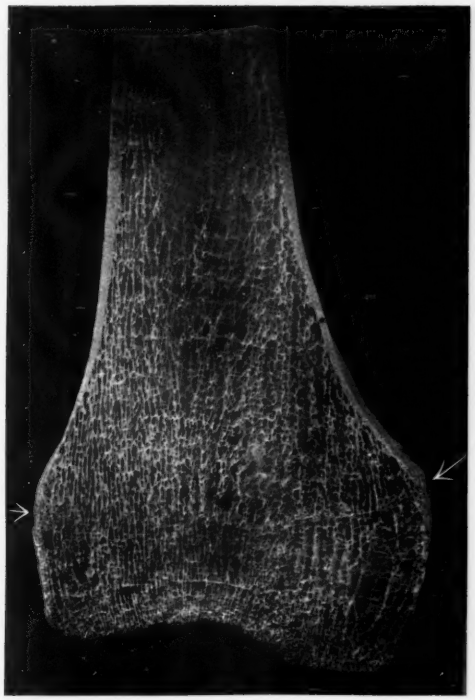


Fig. 2. Coronal section of lower end of femur from a full grown adult (R.C.S. Museum).

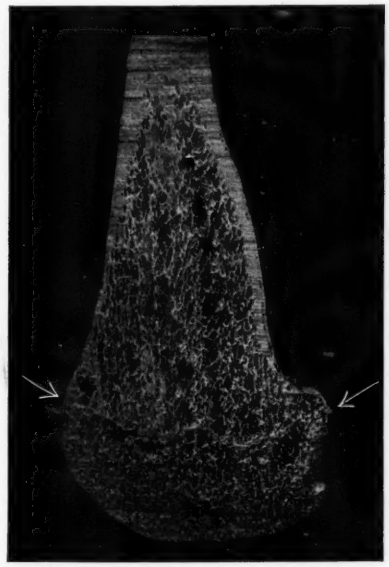


Fig. 3. Sagittal section of lower end of femur from a full grown adult (R.C.S. Museum).

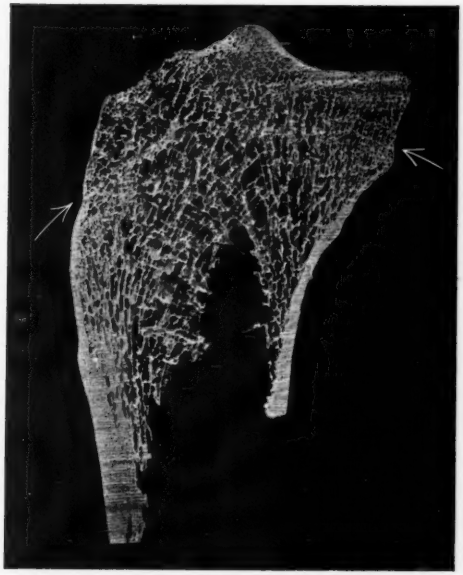


Fig. 4. Section of upper end of tibia from a full grown adult (R.C.S. Museum).

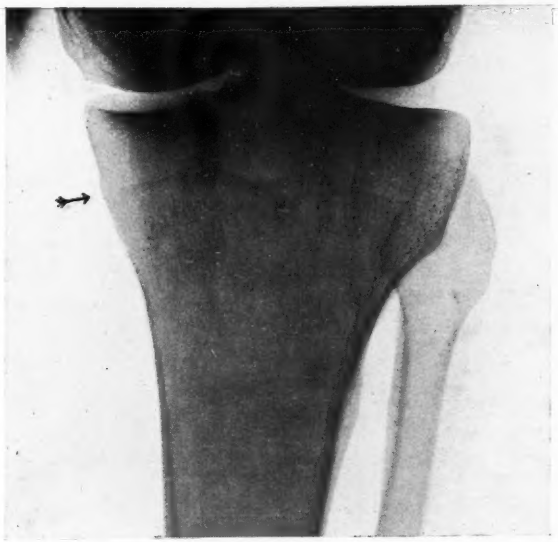


Fig. 5. X-ray of upper end of tibia in a patient aged 60 years, showing fusion-line.

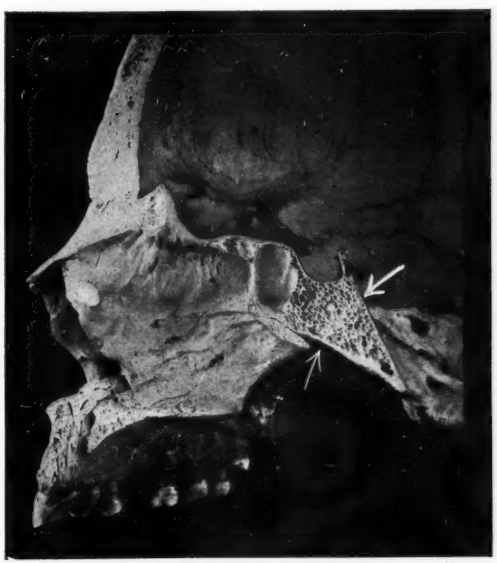


Fig. 6. Sagittal section of skull showing fusion-line between basi-occipital and basi-sphenoid (R.C.S. Museum).

In the skull base the junction between the basi-occipital and the basi-sphenoid can frequently be observed as a band of dense cancellous tissue (fig. 6). The fusion between the segments of the sacrum and of the sternum is also denoted by lines of denser bone. The above facts are sufficient to support the statement made in my former communication.

It is doubtful whether the epiphyseal fusion-line has much clinical importance. It is well known that the cartilaginous epiphysis presents a barrier to the progress of infection and malignant disease, but so far I have been able to find very little evidence that the bony fusion-line acts in a similar manner. In several femora, however, taken from subjects with osteitis deformans, I have noted that the osteoporotic process either stopped short at or left unaffected, the narrow band of denser bone at the junctions of the diaphysis with the epiphyses. That the denser bone has an influence on the formation of air sinuses is easily understood and not difficult to demonstrate.

NOTE ON THE VERTEBRAL EPIPHYSEAL DISCS

By Professor A. FRANCIS DIXON,

Trinity College, Dublin

As is well known the vertebral epiphyseal discs in man are feebly developed structures in comparison with those found in lower animals, and possess an annular and not a complete disc-like outline. A careful examination shows, however, that in one remarkable detail the human epiphyseal plates exhibit an almost complete agreement with those of lower forms.

If a number of young human subjects are examined it will be found that, in the thoracic region, the vertebral epiphyseal plates tend to become first fused to the vertebral bodies in the neighbourhood of the costal facets. In stages a little earlier in development it will be seen that the edges of plates not only cover the upper and under aspects of the vertebral bodies but that they send downwards, or upwards, as the case may be, thin scale-like prolongations to cover the costal articular facets. Even in the three lower thoracic vertebrae, where the costal facets lie far from the upper and lower edges of the vertebral bodies, a slender spicule of bone may often be recognised connecting the articular surface for the head of the rib with the upper epiphyseal vertebral plate of the vertebra.

In this way it can be shown that the costal articular facets, seen in the adult to lie in the vertebral bodies, do not actually belong to those bodies, but are extensions of the vertebral epiphyseal plates. The heads of the ribs articulate not with the bodies of the vertebrae but with their epiphyses. The reason that this fact has been so often overlooked seems to be that the condition is only clearly seen in man for a very short period in the developmental history of the vertebra, and that the fusion of the plate with the vertebral body takes place in the first instance in that part which covers the costal facet. Fig. 1 illustrates the condition in man just at the time when it is best marked.

When we examine the thoracic vertebrae in lower animals the arrangement is much more distinct. The epiphyseal plates are seen to possess wing-like extensions which cover over, and indeed form, the costal facets. The heads of the ribs articulate the epiphyseal plates only (fig. 2). This plan appears to be universal in all animals in which the heads of the ribs reach the main part of the vertebral axis. Man as we have seen is no exception.

One other point is of interest. The annular outline of the human epiphyseal plate arises from a want of ossification in the central part of the cartilage covering the surface of the vertebral body. In such an animal as the baboon we seem to have an intermediate condition between the human type and

that which obtains in quadruped Mammals. In the baboon, as fig. 3 shows, the annular epiphyseal plate is well developed, but in addition a second centre of ossification is seen on the upper and under aspect of the vertebral body, occupying the space enclosed within the annulus. At a stage a little

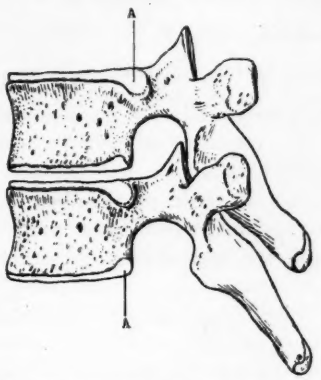


Fig. 1. Two young human thoracic vertebrae. The extension of the vertebral epiphyseal plates to form the costal facets is shown at *A*.

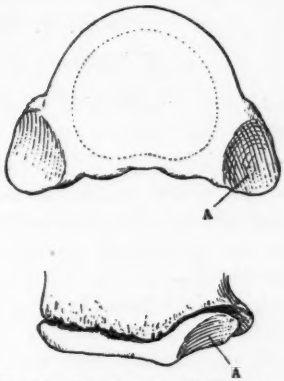


Fig. 2. Vertebral epiphyseal plate from a young Zebu seen from below and from the side. The wing-like extension which forms a part of the articulation for the head of a rib is seen at *A*.

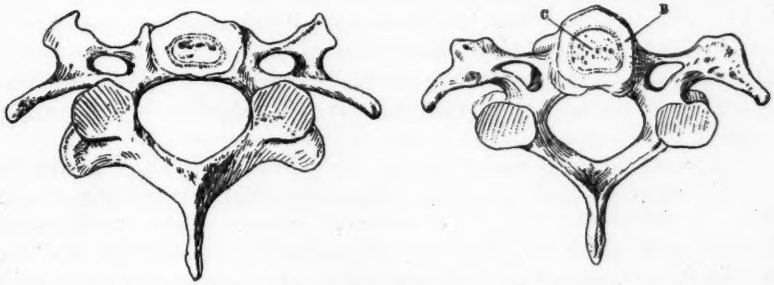


Fig. 3. Cervical vertebra from a young baboon; seen from above and from below. The annular vertebral epiphysis is indicated by *B*, and the ossific islet which arises inside this ring-like epiphysis by *C*.

later in development there may appear to be a complete disc, very thin however in its central portion. Possibly it is the failure of this central ossific islet, *C* in fig. 3, which is responsible for the typical annular form assumed by the human epiphyseal vertebral plates.

ON THE PACCHIONIAN BODIES

By W. E. LE GROS CLARK, F.R.C.S.,

St Thomas's Hospital Medical School, London

The villous outgrowths of the arachnoid membrane in the neighbourhood of the intracranial venous sinuses, which were originally described in detail by Pacchioni (1) in 1721, have for a long time attracted the curiosity of anatomists and physiologists. Investigations of these granulations have almost always been approached from the experimental point of view, and there are surprisingly few observations recorded on their anatomical structure and relations.

Originally referred to as "glandulae" by the old anatomists, the Pacchionian bodies were later regarded as passive filters through which the cerebrospinal fluid drained from the subarachnoid space into the intracranial venous sinuses. This view was strongly supported by the classic work of Key and Retzius (2), and received further corroboration from a number of investigators (3), (4) who approached the problem by different methods of experimental injection.

Latterly, the observations made by Weed (5) enable one to accept, though in a somewhat modified form, the filtration hypothesis as being fully confirmed.

Luschka (6) first pointed out that the Pacchionian bodies are hypertrophied arachnoid villi which are normally present in all brains, but which are microscopic in character. If this is so, then what is the significance of the hypertrophy?

Some authors, among whom are Weed and Rokitansky, regard the granulations as definitely pathological formations. This view appears untenable when consideration is given to the constant presence of the granulations in human brains above a certain age, and to their presence in the brains of certain lower mammals. Weed says that "undoubtedly the Pacchionian granule must be considered as a large hypertrophic villus becoming evident on macroscopic examination in *most*[1] adults." I have never seen an adult in which they were absent.

In order to arrive at a satisfactory solution of the question, it is necessary to enquire more closely into the morphological features of the Pacchionian bodies, and to this aspect of the subject I shall confine myself in the present communication.

The intimate relation—physiological and anatomical—between the development of the arachnoid outgrowths and the venous system is well known, and it is clear that the two must be studied in conjunction.

[1] Italics mine.

During the course of my investigations, I have found that the arrangement of the meningeal venous sinuses and the cerebral veins differs fundamentally in several points from the orthodox description as given in current text-books of anatomy. I propose first to deal with these points, and subsequently to give an account of the macroscopic and microscopic features of the Pacchionian bodies.

A. THE VENOUS SYSTEM IN RELATION TO THE PACCHIONIAN BODIES

1. *The Superior Cortical Veins*

The general course and distribution of these veins have lately been described in some detail by Sargent(7). In common with modern text-books, he describes these veins as sometimes opening into the sagittal sinus directly, and sometimes opening into the lacunae laterales. This statement, I believe, is incorrect, and is based on a misconception of the true nature of the lacunae laterales, as I shall indicate.

If the cortical veins are carefully dissected out, either in injected or uninjected specimens, they will be found always to open directly into the sinus, and never into the cavities of the lacunae. Where they come into relation with the lacunae, the cortical veins pass beneath them. Such at least is the result of my observations which are based on the examination of over 40 brains. It is evident, therefore, that a cerebral vein opening into a lacuna lateralis is a very rare and abnormal occurrence.

In many cases the vein, immediately before opening into the sinus, undergoes a dilatation, and this may be mistaken for a lacuna lateralis. These two structures are, however, situated in different planes, and, moreover, differ in their naked-eye appearance and in their mode of formation.

The floor of the vein is throughout lined by a smooth endothelial membrane which is only very exceptionally perforated by an isolated Pacchionian body near its termination.

The floor of a lacuna, on the other hand, presents a fasciculated appearance, and is usually perforated by numerous arachnoid protrusions, while the cavity is crossed by innumerable fine dural strands. The membrane separating the lumen of the vein from the lacuna may be extremely thin, and is thus readily torn.

2. *The Lacunae Laterales*

These structures develope pari passu with the growth of the Pacchionian bodies, but it is impossible to say precisely when these lacunae—as such—appear in the human brain.

If the intracranial venous system of a new-born child be injected with coloured gelatine, and if the dura mater be then removed, dehydrated with alcohol and cleared in xylol, the following arrangement will be well seen.

Alongside the sagittal sinus is a coarse plexus formed by the anastomosis

of the terminal arborizations of the meningeal veins, the diploic veins which run from the parietal bones to the dura in this region, and the small lateral tributaries of the sagittal sinus.

This plexus occupies precisely the position of, and is formed in exactly the same way as, the lacunae laterales of the adult. As growth proceeds, the venous network becomes more complex, and by the attenuation of the dural meshes and the corresponding widening and coalescence of the venous channels, "lacunae" of variable number and extent are formed.

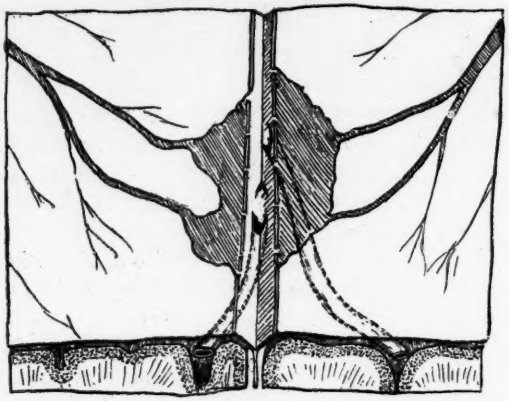


Fig. 1. Diagram illustrating the relations of the cortical and meningeal veins to the lacunae laterales.

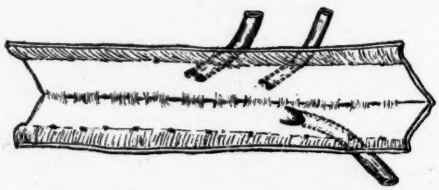


Fig. 2. Diagram illustrating the sagittal sinus laid open from above, to show the openings of the cortical veins and the dural venous plexus.

These lacunae should not be described as well-defined single cavities—diverticula of the sagittal sinus—but rather as a complicated meshwork of veins. If they are studied by dissection, or, better still, microscopically by means of serial sections, it will be seen that the superior terminations of the meningeal veins drain into the outer border of this meshwork, while the diploic veins enter it on its upper aspect. Internally, the meshwork opens by a series of small foramina into the sagittal sinus, i.e. through the venous tributaries of the sinus mentioned in connection with the venous plexus found at birth. The position of these openings is shown with diagrammatic clearness in the sinus of a new-born child, and the accompanying illustration shows their relation to the openings of the cortical veins.

A glance at the calvarium of an adult will show the very numerous diploic foramina scattered alongside the groove for the sagittal sinus, indicating the extent to which the diploic veins enter into the formation of the lacunae laterales.

Faivre (13), indeed, appears to have regarded the lacunae as being formed wholly in association with the diploic veins, for he speaks of "les lacunes, des sinus secondaires qui reçoivent le sang des veines diploïques."

Incidentally, it is perhaps worth while drawing attention to the inadequate description of the openings of the diploic channels as given in anatomy text-books. These descriptions lead the student to suppose that the diploic veins leave the diploë at very few and limited points.

The lacunae, as they increase in size, form small smooth depressions in the frontal and parietal bones on either side of the groove for the sagittal sinus. These are commonly described as "depressions for the Pacchionian bodies." They are more correctly regarded as depressions for the lacunae laterales, for they are frequently well-developed before the Pacchionian bodies are large enough to make an impression on the bone. As the Pacchionian bodies grow, however, they may become lodged in well-defined and sharp-edged pits which can be easily recognised and distinguished by their characteristic appearance. The arrangement of the other cerebral veins and dural sinuses accord well with the usual description. Sargent has recorded the presence of a dilatation at the commencement of the straight sinus, i.e. at the junction of the great vein of Galen and the inferior longitudinal sinus. This dilatation he terms a lacuna, but it is clear that it differs fundamentally in its anatomical relations and mode of formation from the lacunae laterales. This dilatation is especially well marked at birth, when it forms a relatively very large cavity.

B. MACROSCOPIC ANATOMY OF THE PACCHIONIAN BODIES

1. *Development*

The Pacchionian bodies appear at a much earlier age than is generally supposed. At birth they are imperceptible even on examination with a hand lens. At the age of six months they are still invisible, but by 18 months they are quite obvious on close inspection. They appear in the first instance in the regions where the parieto-occipital and central veins open into the sagittal sinus. From these nuclei they spread forwards and backwards along the superior margin of the cerebral hemispheres, and at the age of three they are disseminated over a considerable area. By this time they are often to be seen along the lateral sinuses, on the margin of the cerebellum. At four they project well into the sagittal sinus, forming conspicuous nodules in the lumen of the sinus[1].

[1] Faivre (13) states: "c'est vers la dixième année que ces produits (Pacch. bodies) commencent à se montrer, bien qu'on en puisse trouver avant cette époque." I cannot explain this discrepancy.

2. *Distribution of Pacchionian bodies in Adult*

According to Key and Retzius, the Pacchionian bodies occur in the following situations in order of frequency: sup. longitudinal sinus, transverse sinus, cavernous sinus, sup. petrosal sinus, and venae meningiae mediae. I have also found them in connection with the sphenoparietal and straight sinuses. In all these situations, they tend to congregate in the regions where the cerebral veins open into the sinuses.

In the neighbourhood of the sagittal sinus, the granulations are most numerous in the floor of the lacunae laterales. As these latter increase in extent, the granulations also spread, and, with advancing age, they tend to crawl down the middle meningeal veins. Elliot Smith (8) has recorded an extreme instance of this latter arrangement.

Fig. 3. Section showing Pacchionian bodies in the region of the parieto-occipital fissure in a child aet. 2¼.

The bodies that project into the lumen of the sinus are found in the floor and lateral walls. Quite frequently, a small clump of granulations is found on the floor of the sinus at the mouth of one of the cerebral veins, so that they are bathed by the blood as it is poured from this vein into the sinus.

The Pacchionian bodies in relation to the lateral sinus are practically always confined to the surface of the cerebellum—that is to say, they project into the sinus from below. Very rarely are they found on the surface of the cerebrum in this situation. They are most numerous at the point where the inf. cerebellar veins open into the lateral sinuses on either side of the Torcular Herophili, and from this point they gradually fade away laterally.

The Pacchionian bodies are much less frequently seen in relation to the other venous sinuses, and these become conspicuous only in certain conditions, such as senility.

The precise relation of the Pacchionian bodies to the venous spaces with which they are associated is of some interest. The impression is gained from most descriptions that the Pacchionian bodies are formed by a pouching out of the arachnoid membrane, which eventually finds its way into a venous sinus, i.e. that the body, when it first appears, is not connected with a venous space in the dura. This idea can be readily demonstrated to be erroneous. If the brain, either of an adult or a child, be examined, and if the dura mater be lifted up from the underlying arachnoid with the utmost care, it will be found that every granulation of the arachnoid—even the most minute—is directly attached to the under surface of the dura mater. If this adhesion be broken down and the dura inspected, it will be seen that the point of attachment at the dura is marked by a minute aperture, and with appropriate pressure, blood can be squeezed out through this aperture from the dural

sinuses. This observation—in conjunction with histological evidence to be presently produced—indicates that the arachnoid granulations come into direct contact with the blood of the venous spaces from their first appearance. Poirier (9) wonders "comment functionnent celles qui ne sont pas dans une cavité veineuse." The answer is that they all reach a venous cavity.

Other points in the naked-eye anatomy of the granulations are well-known, and need not be detailed here.

C. MICROSCOPIC ANATOMY OF THE PACCHIONIAN BODIES

Histologically, a Pacchionian body or arachnoid granulation (Arachnoidealzotte of German authors) appears as a diverticulum of the subarachnoid space penetrating into the interstices of the dura mater. It is thus covered by a layer of arachnoid mesothelium, and contains a prolongation of the subarachnoid space.

The arachnoid mesothelium consists of a single layer of flattened cells, with lightly staining cytoplasm and large oval nuclei. The subarachnoid space consists of a reticulum of fine fibrous tissue in which are scattered a number of connective-tissue cells. These cells are most numerous, and the fibrous stroma more dense, immediately beneath the arachnoid mesothelium, and on the surface of the brain. Between these two areas, bundles of fine fibrous tissue predominate and the cellular element is very scanty. In children, these connective-tissue cells are found in very much larger numbers, and intertrabecular spaces are very much less marked than in adults.

Incidentally, it may be noted that the pia mater is merely a condensation of the subarachnoid trabecular tissue, and is not a definite membrane comparable to the arachnoid. The density of the subarachnoid tissue in the Pacchionian bodies as a rule is greater at the periphery than at the centre of the structure, and this difference is more marked in the larger granulations.

Although not usual, it is by no means uncommon to find a small capillary blood-vessel in the cavity of a granulation, and in some cases a capillary may be observed to leave the granulation by passing through the arachnoid mesothelium and subdural space to reach the surrounding dura mater. In the Pacchionian bodies of adults, and more so in advanced age, there are frequently found small calcareous nodules. These may be either spherical or cylindrical in shape. They appear to arise by the calcification of small collections of endothelial cells arranged in a concentric formation. My sections show these latter structures undergoing various degrees of hyaline and calcareous changes to form ultimately calcareous nodules. The origin of the primary endothelial formation is, however, not clear. Some sections would appear to indicate their origin in connection with capillary blood-vessels by a proliferation of the endothelium. In other sections they are found in the epithelial cap on the summit of the Pacchionian body, as described below. Their interest lies in the close resemblance of their structure to that

of endotheliomatous tumours in this region, and this fact lends support to the suggestion—originally put forward by Schmidt (11) with detailed evidence—that the so-called endotheliomata of the dura mater are really arachnoidal tumours. The calcareous changes in these endotheliomata leading to the formation of psammomata are well-known.

If the arachnoid mesothelium of a Pacchionian body be followed throughout the structure by means of serial sections, it will be found that at the summit of the granulations the mesothelial cells proliferate to form a multilayered cellular cap, and this cellular formation penetrates the surrounding dura mater to come into direct continuity with the endothelial lining of the

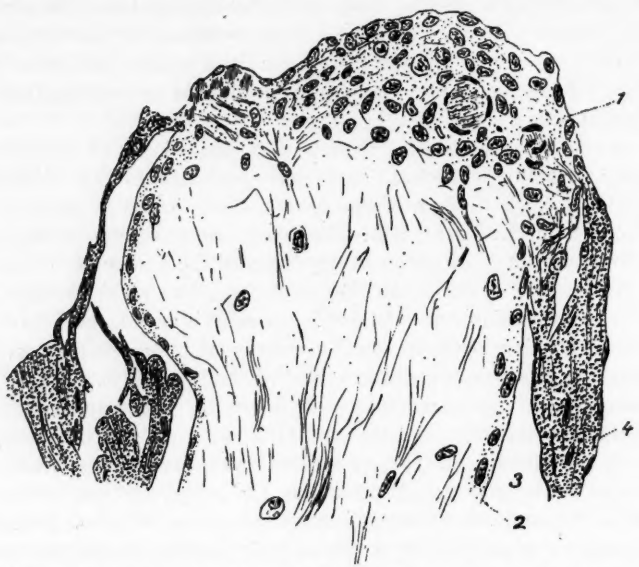


Fig. 4. Section 49, showing tip of Pacchionian body projecting into a venous sinus. The arachnoid has completely blended with the vascular endothelium, and the subdural space is obliterated. 1. Epithelial cap. 2. Arachnoid mesothelium. 3. Subdural space. 4. Dura mater.

intradural venous sinuses. At this point, that is to say, there is no subdural space or layer of dura mater intervening between the arachnoid and the venous sinus.

This mesothelial cap is evidently identical in structure with the cellular tuft described by Weed in connection with the microscopic arachnoid villi of lower animals, and corresponds to the "Epithelzapfen" of German authors (10, 11). Moreover, Weed (5) has demonstrated that it is through this structure that the cerebro-spinal fluid passes from the subarachnoid space into the venous sinuses.

Except for this point of fusion between the arachnoid and the vascular endothelium (which can be demonstrated by serial sections), the arachnoid

covering the Pacchionian bodies is surrounded by the subdural space and the dura mater. The latter—covered on its cerebral aspect by a layer of endothelium—is invaginated into the venous sinus by the protrusion of the arachnoid granulation. In most sections of a Pacchionian body it appears to be completely surrounded by the subdural space, but, as pointed out above, this is not so.

Histological evidence indicates that the Pacchionian bodies are developed in the following way. Opposite the point where an intradural venous sinus approaches the cerebral surface of the dura mater, the arachnoid cells proliferate to form a cell cluster (Epithelknoten of German authors). The cellular tuft thus formed finds its way through the interstices of the thin layer of dura mater separating it from the sinus, and fuses with the endothelial lining of the latter. In so doing, it pulls out a stalk of arachnoid membrane con-

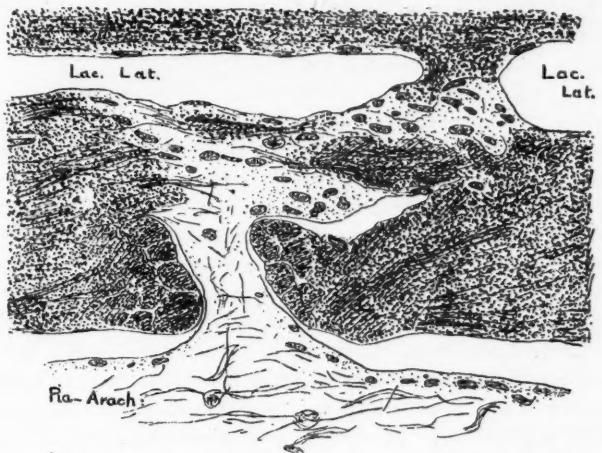


Fig. 5. Section 102, showing the first formation of an arachnoid villus.

taining a diverticulum of the subarachnoid space. This early stage is shown in the accompanying illustration.

Thus is formed the microscopic arachnoid villus normally present in all brains. Subsequent growth, leading to the formation of the macroscopic arachnoid granulation, appears to take place almost entirely by the dilatation of the subarachnoid space in the pedicle of the microscopic villus.

D. SIGNIFICANCE OF THE PACCHIONIAN BODIES

The assumption that the Pacchionian bodies constitute the essential mechanism of filtration of the cerebro-spinal fluid is nullified by Weed's researches. He has shown that the cerebro-spinal fluid reaches the venous channels by means of the microscopic arachnoid villi. It therefore remains to ascertain the precise relation of the Pacchionian bodies to the villi.

Microscopic examination gives the Pacchionian bodies the appearance of arachnoid villi which have been distended and herniated into the cavity

of the venous sinuses by the pressure of the cerebro-spinal fluid. And it is, in fact, suggested that the size and number of the Pacchionian bodies are an indication of the cerebro-spinal fluid pressure. If this is the case, then an examination of the brain of an individual who has died with an abnormally high cerebro-spinal fluid pressure should reveal an unusual development of the Pacchionian bodies. This indeed appears to be the case. It is well known that an autopsy of a case of Dementia Paralytica reveals an increase in the number and size of the Pacchionian bodies (Stoddart(16)). This is correlated with an increased pressure of the cerebro-spinal fluid, for an examination of the brain also shows that "the sulci are distended with fluid" (Mott(14)).

Similar changes are to be found in cases where the intracranial pressure is raised by the presence of tumours. I have lately seen the post-mortem examination of a case of cerebral tumour in which there was evidence of increased intracranial pressure of two years standing. In this case, the Pacchionian bodies were very clearly larger and more numerous than in a normal person of the same age and sex.

Again, the Pacchionian bodies are always found to be very well developed —sometimes to an extraordinary degree—in patients suffering from chronic nephritis and arterio-sclerosis. In these cases, the arterial blood-pressure is abnormally high, and it has been shown that the cerebro-spinal fluid pressure is dependent to a certain extent upon the blood-pressure (Becht(15)). If the development of the Pacchionian bodies is indeed an expression of the cerebro-spinal fluid pressure, then the increase in number and size of these bodies with advancing age receives a satisfactory explanation. For the blood-pressure increases with age, and presumably therefore the pressure of the cerebro-spinal fluid also rises.

It is thus seen that the Pacchionian granule is not so much an hypertrophy as a distension of the arachnoid villus, and it appears that Pacchioni was correct in his implication: "In senibus vero glandulae albescentes et magis turgidae cernuntur."

REFERENCES

(1) Pacchioni. *Dissertationes Physico-anatomicae de Dura Meninge Humana.* 1721.
(2) Key and Retzius. *Anatomie des Nervensystems und des Bindesgewebe.* Stockholm, 1876.
(3) Leonard Hill. *Physiology and Pathology of the Cerebral Circulation.* 1896.
(4) Spina. "Experimentelle Untersuchungen über die Bildung des Liquor cerebrospinalis." *Arch. f. d. gesammte Physiol.* LXXVI. 1899.
(5) Weed. *J. of Medical Research,* XXXI. 1914.
(6) Luschka. *Die Adergeflechte des Menschlichen Gehirns.* 1855.
(7) Sargent. "Some Points in the Anatomy of the Intracranial Blood Sinuses." *J. of Anat. and Phys.* XLV.
(8) Elliot Smith. *Rev. Neur. and Psych.* March, 1905.
(9) Poirier and Charpy. *Traité d'Anatomie humaine.* 1907.
(10) Bluntschli. *Verhandl. Gesellsch. deutsch. Nat. Aertz. Verein.* 80 Th. 2 Hälfte, 2, p. 363, 1909.
(11) Schmidt. "Ueber die Pacchionischen Granulationen und ihr Verhältniss zu den Sarcomen und Psammomen der Dura Mater." *Arch. f. Path. Anat.* Berlin, 1912, CLXX. 429.
(12) Cushing. *Am. J. of Med. Sciences,* CXXIV. No. 3, 1902.
(13) Faivre. "Les granulations méningiennes." Collection des Thèses. *École de Médecine.* Paris, 1853.
(14) Mott. *General Pathology* (ed. by Pembrey and Ritchie). 1913.
(15) Becht. *Amer. Journ. of Physiology,* LI. No. 1, 1920.
(16) Stoddart. *Mind and its Disorders.*

NOTE ON THE LACHRYMAL GLAND OF THE HEDGEHOG

By E. W. HURST, B.Sc.

From the Physiological Laboratories of the University of Birmingham

METHODS OF PREPARATION

The animals were killed with coal gas and portions of the tissues fixed in one of the following fixatives:

Mann's solution (B) (7),
Flemming's Chromo-osmo-acetic acid,
Mercuric chloride.

Subsequently sections were made from these by the methods in common use, and stained with well-known dyes.

LITERATURE

Langley (5) describes the lachrymal of the rabbit as corresponding to the infra-orbital. He states that it is difficult to distinguish between the two, but that they are not usually active at the same time. The cells show an outer clear and an inner granular zone during activity.

Dahlgren and Kepner (3) describe the lachrymal of the mouse as appearing on first sight like the sebaceous tissue of the chicken's rump. The cells, however, form a single layer, and there is no obvious method of renewal. The secretion appears in little globules or vacuoles in the proximal end of the cell and moves through or with the cytoplasm to the distal end, where it is set free with a disintegrating part of the cytoplasm, the nucleus remaining at the proximal end of the cell. The secretion stains black with osmic acid, but is not a true fat because it is soluble in water.

Szymonowicz (10) states that the ducts consist of a basement membrane surrounded by star-shaped cells that form a network around it: they are lined by cylindrical epithelium, which is prolonged into the acini.

Dogiel (4) says that the basement membrane of the tubules is surrounded by a basket work of nerve fibres, from which finer fibres pierce the membrane to form a network around the bases of the cells, and another between the cells.

Thanhoffer (11) maintains that the lachrymal gland is wanting in those vertebrates that have no eyelids, but is present in serpents.

Lowenthal (6) mentions in his work on the development of the orbital glands that in the hedgehog the lachrymal and the infra-orbitals develop

from the conjunctival sacs, but in the guinea-pig the latter develops from the lachrymal.

Schäfer (9) in *Quain's Anatomy* describes the gland as compound tubulo-racemose with the tubules enlarged at the closed ends (Marziarski). The cells are situated upon a basement membrane of flattened cells, outside which again there is plain muscle in both ducts (Zimmermann (12)) and alveoli (Kolossow). The cells lining the ducts are columnar, but do not exhibit any rodding, which is such a characteristic feature of salivary duct cells. In old age the interglandular tissue becomes crowded with lymph cells.

According to Noll (8) there are two kinds of cells present in the lachrymal gland, one of which stains lightly and exhibits an evident cell network, the other staining darkly and so obscuring the cyto-reticulum which is no doubt there however; there are also cells present which in staining lie intermediate between the two extremes. He finds that on stimulating the glands, the cells undergo certain marked changes and exhibit droplets of fat that stain with osmic acid and intensely red staining small granules often in increasing number. The cell network, so evident in the resting gland cell, is absent from most of them after stimulation.

DISSECTION

The orbit of one animal was carefully dissected to expose its contents, when the eyeball was seen to be surrounded by four glandular masses distinctly separated from one another. These have been designated in the accompanying figure as *A*, *B*, *C*, *D*; of these *A* only is a true lachrymal, and even to the unaided eye differs in appearance from the others, as it presents a smooth surface; the others *B*, *C*, *D* are lobulated and are of the nature of salivary glands, so constituting the orbital gland of this animal.

Fig. 1. Dissection of the orbit of a hedgehog to show the position of the various gland masses. *A*. Lachrymal. *B, C, D*. Orbital.

After being photographed each gland mass was carefully removed and placed in a separate receptacle, in which it was fixed and taken through the usual processes for microscopical examination, in order to determine its nature, with the result already stated.

Sufficient attention does not appear to have been paid by some authors to this difference in the gland masses present in the orbit and so some confusion has arisen in the descriptions they have given of lachrymal cell structure.

STRUCTURE OF THE LACHRYMAL GLAND

In the resting condition

In most of the animals examined the glands were active, but in one killed during hibernation the glands were certainly in a resting condition.

In the hedgehog the gland differs from that of all other animals examined by me in its diffuse appearance (fig. 2), which is caused by the tubules being arranged either singly or in twos and threes, widely separated from one another by adipose tissue, the fat of which reacts acid to nile blue, as the fat of adipose tissue elsewhere in the body does.

Surrounding the whole gland is a thin fibrous capsule, that lies in close relation to the orbital glands and muscles. From this capsule septa pass inwards into the gland to unite with prolongations of the capsule carried in around the vessels and ducts.

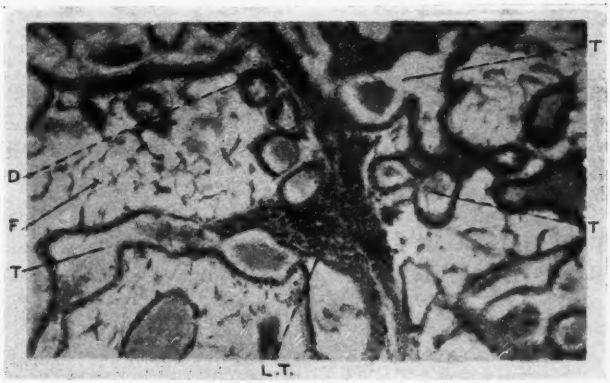


Fig. 2. Low power view of resting gland. *T.* = tubules. *D.* = duct. *L.T.* = lymphoid tissue. *F.* = fat.

The acini, which are circular, oval, or polyhedral in shape, vary considerably in size with an average diameter of 110μ, that of the lumen being 75μ: but many greatly exceed this, and may reach double the average size. The tubules are wider at their closed ends, as described by Marziarski, see *Quain's Anatomy* (9), than where they open into the ducts.

In many cases the wide lumen of the acinus is filled with a coagulated mass of protein nature, containing large droplets that stain black with osmic acid, and nuclei derived from the cells are often present in it. The cells lining the acini are of cubical or low columnar shape, measure 13μ in height, and present flattened extremities to the lumen (fig. 3). Their cytoplasm is cloudy and the cell outlines indistinct. With methyl blue eosine (7) many small eosinophile granules are seen in the neighbourhood of the nucleus, as described in *Quain* (9), and in addition some larger clearer bodies (described in the same article as clear granules with no definite affinity for stains) are present in some number

near the free end of the cell, but vary greatly both in size and number in different cells. The spherical nucleus which lies in the centre and outer part of the cell is of comparatively large size, measuring 6μ in diameter, which is half that of the cell itself. Its chromatin content lies chiefly at the periphery, which gives it a clear appearance, and it often contains a nucleolus. In cases in which the accumulated secretion has distended the acinus (storage secretion) the lining cells are reduced to flattened squames. The cells are arranged in a single layer and stand upon an endothelial basement membrane, which, in many cases, seems to be the only fibrous structure present. The supporting wall of the acinus is therefore often of extreme tenuity, and the tubule must depend for its support largely upon the fatty tissue in which it lies, though the fatty tissue may equally well be considered as having been developed from the walls and fibrous tissue between the acini.

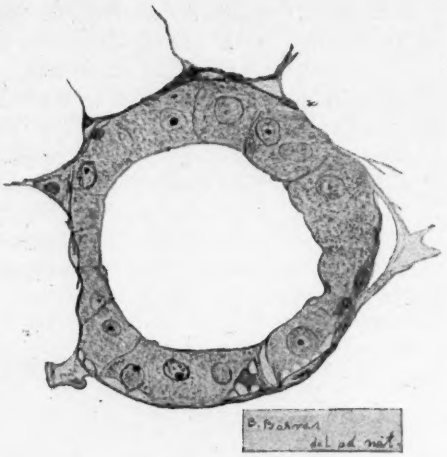


Fig. 3. Lachrymal gland of hedgehog in the resting condition.

The larger ducts are lined by a single layer of columnar cells with oval nuclei of considerable size, the chromatin content of which is greater than in those of the acini. Here and there among them are one or two well marked goblet cells, an occurrence which does not seem to have been hitherto recorded and which may not be found in the same situations in other animals. This may be merely another case in which mucous secreting structures are present in the hedgehog in an unusual place, for have not mucous glands been described by Carlier (1) in the pancreatic duct of this species!

The smaller ducts are lined by cubical cells, among which there do not appear to be any goblet cells. Where the ducts join the acini the cells seem to be prolonged into them for some little distance, as described by Szymonowicz (10). There is an endotheloid basement membrane outside the lining epithelium of all the ducts, but of the stellate cells mentioned by Szymonowicz (10) no trace can be found. Outside the basement membrane is ordinary connective tissue, containing here and there a few non-striped muscle fibres circularly disposed as mentioned in *Quain* (9). Thick walled vessels and, occasionally, some lymphoid tissue may be seen in the fibrous sheaths.

In the active condition

When the animals become active after hibernation and throughout the early summer the gland tubules appear more numerous and more closely packed together, probably because there is then less fat in these animals than during their long winter sleep. When the glands secrete, the lining cells of the acini become much higher, measuring on an average 30μ, which is about two and a half times their former height, and their free extremities become very ragged, giving to the lumen an irregular outline. Many vacuoles, varying much in size, are present in the cytoplasm, producing a honeycomb appearance, more nearly resembling those seen in mammary gland cells than those of the lachrymal cells of the rabbit and guinea-pig, in which animals

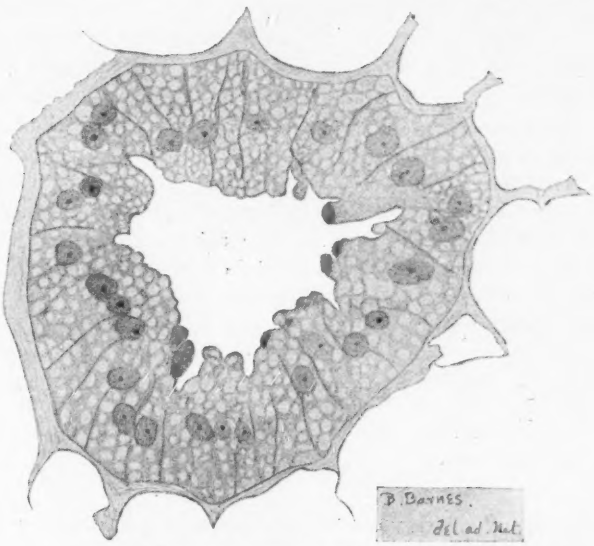


Fig 4. Lachrymal gland of hedgehog in full activity.

the vacuoles, being nearly all of one size, produce a beautiful reticulate appearance throughout the cell (fig. 4). When treated with osmic acid their contents stain a blackish colour, as noted by Dahlgren and Kepner (3), who state that the blackened substance is soluble in water, and therefore cannot be of a fatty nature. This would also appear to be the case here, as it does not react in the least to nile blue and other specific fat stains.

Both kinds of granules found in the resting cells seem to disappear from the cytoplasm during secretion, and the cell outlines become distinct. Here and there portions of the cell, sometimes vacuolated, sometimes not, can be seen breaking off and passing into the lumen of the acinus. These disrupted parts stain more deeply than the remainder of the cell, as described by Dahlgren

and Kepner (3). This peculiarity further increases the resemblance which these cells bear to those of an active mammary gland.

During this activity the nuclei are slightly swollen, measure 7 μ in diameter, appear clouded and come to lie close to the lumen. They react differently to methyl blue eosine, some uniting with the blue and others with the red stain. This may merely indicate that all the cells are not in the same state of activity at the same time; probably they work in relays, or it may indicate various stages of nuclear exhaustion as described by Carlier (2). With other dyes such as iron alum haematoxylin, different nuclei stain with different intensity. The nucleoli are larger and more numerous than in the resting condition and some may be seen bodily extruded into the cytoplasm where they break down.

There seems to be no evidence of the two distinct kinds of cells in the glands of the hedgehog, described by Noll (8) as present in lachrymal glands generally, though as pointed out by him, cells the cytoplasm of which does not stain uniformly may be seen in some acini mingled with the others. This appearance would seem to be due to a less even distribution of the clear granules throughout the cell, than usually obtains.

In the gland masses *B*, *C*, *D* (orbital gland) two kinds of cells, the one clear, and the other dusky, are readily seen and present different affinities for the various dyes, the cytoplasm of the clear being distinctly eosinophile whilst that of the dusky ones seems to contain a basophile material within it.

No trace of the secretion canals described by Schäfer (9) could be found, but lymph corpuscles are numerous, forming patches of various sizes here and there in the connective tissue around the vessels. The ducts show little change beyond an occasional vacuole in the free extremity of the lining cells.

OTHER OBSERVATIONS

In the lachrymal gland of one of the hedgehogs examined a few tubules were found among the others lined not by lachrymal cells, but by serous cells identical with those lining the tubules of the neighbouring orbital gland. This may be merely due to an inclusion of a minute portion of the orbital in the lachrymal during development, but in one single acinus lachrymal and orbital gland cells were placed side by side which would rather point to a common origin for all the glands of the orbit, as suggested by Lowenthal (6), with subsequent differentiation of one of them to form a lachrymal.

REFERENCES

(1) CARLIER. "The Pancreas of the Hedgehog." *Journ. Anat. and Phys.* vol. XXX. p. 334.
(2) —— "Concerning the Secretion of Ferments by the Liver Cells." *La Cellule*, vol. XXII. p. 431.
(3) DAHLGREN and KEPNER. *Textbook of the Principles of Animal Histology.* New York, 1908.
(4) DOGIEL. *Archiv f. Mikro. Anat.* vol. XLIV. 1895.
(5) LANGLEY. "The Infra-orbital Gland of the Rabbit and the Lachrymal Gland of the Rabbit." *Journ. of Physiol.* vol. II. pp. 274–75, 1879–80.
(6) LOWENTHAL. "Drüsenstudien. IV. Beitrag z. Kenntnis d. Entwicklung d. Augenhöhlendrüsen." *Archiv f. Mikro. Anat.* vol. LXXIX. p. 464, 1892.
(7) MANN, G. *Physiological Histology. Methods and Theory.* Oxford, 1902.
(8) NOLL. "Morphologische Veränderungen der Thränendrüse bei der Secretion." *Archiv f. Mikro. Anat.* vol. LVIII. p. 487.
(9) SCHÄFER and SYMINGTON. *Quain's Anatomy*, vol. III. Part II. p. 181, 1909.
(10) SZYMONOWICZ. *Lehrbuch der Histologie und der Mikroskopischen Anatomie mit besonderer Berücksichtigung des menschlichen Körpers einschliesslich der mikroskopischen Technik.* Würzburg, 1901, p. 360.
(11) THANHOFFER. *Grundzüge der vergleichenden Physiologie und Histologie.* Stuttgart. 1885.
(12) ZIMMERMANN. "Beiträge zur Kenntniss einiger Drüsen und Epithelien." *Archiv f. Mikro. Anat.* vol. LII. p. 552.

THE EXACT DISTRIBUTION OF THE GASTRIC GLANDS IN MAN AND IN CERTAIN ANIMALS

By Y. MIYAGAWA, M.D.,
Assistant Prof. of the Med. Faculty of the Imperial University, Tokio

From the University College Hospital Medical School, London

INTRODUCTION

The gastric glands in man and in lower animals are generally classified into three groups, namely: cardiac, fundus and pyloric. The cardiac gland is however not always considered as an independent kind of gastric gland, but as belonging to the fundus group. Some authors describe a few mucous glands, principally in the prepyloric area. The pyloric and fundus glands are the most important forms, from both the pathological and the physiological points of view. The usual statement made with regard to the localization of these forms of gastric glands is that the pyloric glands occupy the pyloric region, the fundus glands the fundus and the body of the stomach, and the cardiac a narrow area surrounding the cardiac orifice. I cannot however find any description which deals with their *exact* distribution. To know this is of capital importance from both physiological and pathological standpoints; for example, from the point of view of the study of the gastric secretion with regard to hydrochloric acid and the ferments, or from that of the study of the localization or genesis of gastric ulcers and of carcinoma, and of their relationship to the various types of gastric glands. The observation of Pawlow, Heidenhain, Edkins and Starling mark epochs in the study of the gastric secretion, but in those researches apparently no definite attention has been paid to the exact distribution of the gastric glands.

In the present investigation I have mapped out the exact distribution of these three types of gastric glands in the stomachs of two adults and one infant, and also in the guinea-pig, rabbit and cat.

METHOD OF INVESTIGATION

The stomach used in this observation was opened in luke-warm physiological salt solution, its contents removed and the mucous membrane thoroughly washed in that solution. It was then stretched and pinned out on cork, thus obliterating the folds of the mucous membrane, and after fixation in 8 per cent. formalin solution was cut into serial sections and stained with haematoxylin and eosin, iron haematoxylin and Van Gieson, methylen blue and fuchsin. For the systematic microscopical examination,

the posterior wall of the stomach was divided into longitudinal strips, each 1 cm. broad and each strip was then cut into blocks 2 cm. long. The blocks were cut into sections in the *longitudinal* direction with a microtome by the paraffin method. The anterior wall was divided into squares as in fig. 1, the number varying according to the size of the animal. These blocks were cut into sections in the *transverse* direction. All the blocks were numbered as in fig. 1 for identification and each block was cut as described above into a complete series of serial sections.

(I) THE EXACT DISTRIBUTION OF THE GASTRIC GLANDS IN THE GUINEA-PIG

A guinea-pig weighing about 350 grams, after twenty hours starvation, was killed by a blow on the neck. Its stomach was examined exactly as above described.

Microscopic Appearances

There was no difference between the distribution of the gastric glands on the anterior and posterior walls, so that they were found to be perfectly symmetrical on the two sides.

The length of the lesser curvature of the stretched stomach used in this experiment was 3·5 cm. and the entire distribution length of the pyloric glands on the lesser curvature,—in which no fundus glands were seen,—was about 1·7 cm. from the pyloro-duodenal border. The ratio of the entire distribution length of the pyloric glands to the total length of the lesser curvature was therefore as 17/35 (approximately 5/10 (+)). The length of this distribution on the greater curvature was practically the same as that on the lesser curvature.

Intermediate zone

The intermediate zone between the pyloric and the fundus glands was nearly 1 mm. in width and took the form of a slight curved line. There was formed in this way a triangle on both the anterior and the posterior walls, corresponding to the area of the pyloric glands.

There was a sudden decrease in the number of the fundus glands and a sudden increase in that of the pyloric glands in the intermediate zone. The gland cells of both kinds were never found intermingled in the same gland tubule, each tubule remaining either entirely of the pyloric or of the fundus type.

Oxyntic Cells

In the pyloric gland area

These were never found in group form, but always occurred irregularly in the body of a pyloric gland, taking a parietal position between the ordinary gland cells, exactly as in the case of the cardiac glands. Contrary to the usual teaching, isolated oxyntic cells were found scattered throughout the whole pyloric gland area.

In the fundus gland area

Oxyntic cells were found of course in the fundus glands in group form as usual, but mostly abounded in the corpus gastricum and prepyloric part, being smaller in number at the fundus extreme.

In the cardiac gland area

The cardiac glands were found in a narrow area in two or three groups immediately surrounding the cardiac orifice and the ordinary gland cells of this part always included a few oxyntic cells.

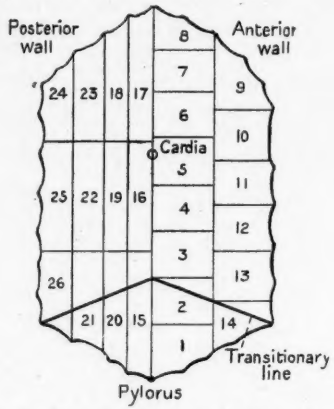


Fig. 1. The stretched stomach of a guinea-pig (divided into areas).

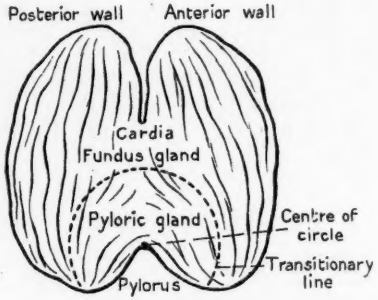


Fig. 2. The stomach of a guinea-pig (opened in luke-warm saline solution).

Macroscopic appearances

The macroscopic appearances of the two parts occupied by the pyloric and fundus glands showed the following characteristics. The area occupied by the former glands was much pinker, the mucous membrane being thicker and tougher and more intimately adherent to and more firmly connected with the underlying tissue than that of the fundus gland area. The lines of the rugae in the mucous membrane are longitudinal and particularly marked along the lesser and greater curvatures in the fundus and the gastric body; but, in the area of the pyloric glands, they are much more oblique or even circular near the pyloric sphincter.

The mucous membrane in the area of the fundus glands is thinner and softer, being of dark brown pink colour, especially in the centre of the body, and its separation from the underlying tissue is quite easy, large lamellae being formed.

The mathematical determination of the distribution area of the pyloric glands

The distribution area of the pyloric glands can be mathematically determined by drawing a circle, having its centre at the pyloric end of the lesser curvature and having a radius equal to the distance from this centre to the mid-point of the lesser curvature. This circle represents the distribution area of the pyloric glands.

(II) THE EXACT DISTRIBUTION OF THE GASTRIC GLANDS IN A NORMAL RABBIT

A large rabbit after 24 hours starvation was killed by a blow on the neck and its stomach opened in luke-warm physiological salt solution. The stomach was stretched and pinned out on cork. After fixation it was cut into serial sections and stained, the same methods being employed as in the case of the guinea-pig.

Microscopic appearances

There was no difference between the distribution of the gastric glands on the anterior and posterior walls,—thus, as in the case of the guinea-pig, they were found to be perfectly symmetrical on the two sides. The lesser curvature in the stretched stomach of this rabbit was 6·5 cm. long and the entire distribution length of the pyloric glands on the lesser curvature—in which no fundus glands were seen,—was about 4·5 cm. from the pyloro-duodenal border. The ratio of the entire distribution length of the pyloric glands to the total length of the lesser curvature may be calculated therefore as 45/65 (approximately 7/10 (+)). The length of this distribution on the greater curvature was practically the same as that on the lesser curvature. The intermediate zone between the pyloric and fundus glands area was nearly 1 mm. in width, taking the form of a line as in the guinea-pig. The distribution area of the pyloric glands is therefore proportionately greater than that of the other animals examined and also of man.

Oxyntic cells. A few isolated oxyntic cells were as in the guinea-pig found in the pyloric glands, never in group form as in the case of the human being, but always in the body of the glands, taking a parietal position between the ordinary gland cells. The same statement applies to the cardiac glands. Oxyntic cells were found as usual in group form in the fundus glands being most abundant in the corpus gastricum and the prepyloric part of the stomach.

The cardiac glands. The condition of the cardiac glands was found to be practically the same as that of the guinea-pig.

The macroscopical characteristic appearances of the distribution area of the pyloric glands

The distribution area of these glands as seen after washing the stomach in salt solution immediately after killing the animal was more whitish-pink

in colour than that of the fundus glands area, which was much darker and brownish-pink in colour. The course of the folds in the mucous membrane was similar to that in the stomach of the guinea-pig. This part had a higher chromaffinity as shown by staining with Müller than that of any other region, especially in the region of the lesser curvature. This region of high chromaffinity extended along the lesser curvature to within 0·5 cm. of the cardia. Furthermore the blood was much more easily washed out from this area than from the fundus gland area, by transfusion of physiological salt solution into the aorta thoracalis. This facility of washing out the blood depends upon the smaller amount of blood in the part and upon the shortness of the vessels supplying it. The mucous membrane was thicker, harder and its separation from the muscularis mucasae was much more difficult than that of the fundus gland area, its connection to the underlying tissue being much firmer.

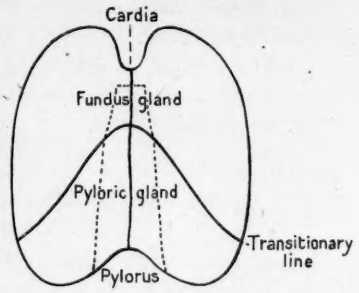


Fig. 3. The stretched stomach of a rabbit. The area shown in dotted line has high chromaffinity.

The mathematical determination of the distribution area of the pyloric glands

The distribution area of the pyloric glands can be mathematically determined by describing a circle, its centre being at the pyloric end of the lesser curvature and its radius equal to a distance of 7/10 of the total length of the lesser curvature. The distribution area represents the area covered by the circle.

(III) THE EXACT DISTRIBUTION OF THE GASTRIC GLANDS IN THE CAT

I have examined the stomach of a large cat by practically the same method as described above. I found the area of distribution of the pyloric glands to extend for a distance of 5 cm. along the lesser curvature from the pylorus and nearly the same length along the greater curvature. In this particular stomach, the total length of the lesser curvature was 12 cm. after stretching and fixation in 8 per cent. formalin solution. The ratio of both lengths may be calculated consequently as 5/12 (approximately 4/10 (−)).

Oxyntic cells. The oxyntic cells were found scattered in small numbers and not in group formation in both the pyloric and the cardiac glands, as described above for the guinea-pig and rabbit. The greater number of the oxyntic cells abounded as usual in the corpus gastricum and the prepyloric part in group formation.

Cardiac glands. The cardiac glands were found in from two to four groups in a narrow area, which surrounded the cardiac orifice. The secreting tubule was much smaller than that of the fundus and the pyloric glands and the ordinary gland cells were columnar and moderately high, being filled with fine granules, which could be always much more intensively stained with dyes than those of the principal cells in the fundus glands. Between the gland cells were found a few oxyntic cells, which were much more numerous than those in the herbivora. Haane's (1) description of the cardiac glands in the cat is as follows: "Bei der Katze liegen die Verhältnisse ungefähr so wie beim Hunde, doch sah ich hier gleich am Oesophagus echte Fundusdrüsen und so kann man wohl annehmen, dass die Katze eine reine Cardiadrüsenzone besitzt, sondern eine intermediäre Zone....Fleischfresser haben eine ganz kleine Cardiadrüsenzone an der Speiseröhrenmündung oder nur eine intermediäre Zone, wo Cardiadrüsen mit Fundusdrüsen gemischt sind. Letztere ist auch dann vorhanden, wenn zugleich eine reine Cardiadrüsenzone zugegen ist. In diesen Zonen kommt noch eine ganz besondere Art von Drüsen vor, nämlich solche, welche mit acidophilen Zellen ausgerüstet sind, aber daneben auch Belegzellen enthalten."

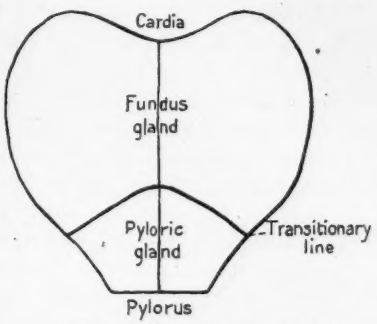


Fig. 4. The stomach of a cat.

At any rate, I have not the slightest doubt in my own mind that the cardiac gland in the cat is an independent kind of gastric gland, because of the staining properties and formation of the tubules.

The macroscopical characteristic appearances of the distribution area of the pyloric glands and its mathematical determination

The colour, toughness and the course of the folds of the mucous membrane in this area were quite similar to the herbivora described above. One can easily determine mathematically this distribution area by use of the ratio 4/10 (+) as described above.

(IV) THE EXACT DISTRIBUTION OF THE GASTRIC GLANDS IN MAN

I have examined three human stomachs, two adults,—one fresh and the other a preserved specimen—and a fresh stomach of a six weeks old infant. There was a slight difference in the gland distribution area between the adults and the infant.

A. (i) The Adult Stomach (*fresh specimen*)

The total length of the lesser curvature was 19 cm. in the freshly stretched and fixed stomach examined and the entire distribution length of the pyloric glands from the pyloric end-point of the lesser curvature was 5·5 cm. on this curvature. The ratio between these lengths may be therefore estimated as 55/190 (approximately 3/10 (+)).

The distances from the middle points of the pyloric sphincter on the anterior and posterior walls to the limit of the pyloric gland area on the lesser curvature were the same as the distances from those two points to the limit of the pyloric gland area on the greater curvature. There was no difference between the distribution of the gastric glands on the anterior and posterior walls, so that they were found to be completely symmetrical on both sides.

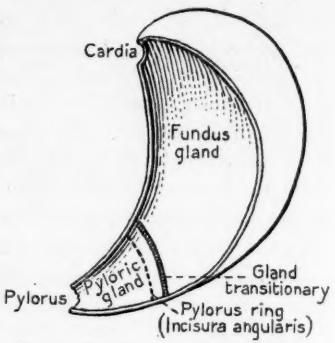


Fig. 5. The human stomach (adult).

The intermediate zone. The intermediate zone between the pyloric and fundus gland areas was nearly 1 cm. in width. The pyloric glands were gradually decreased and the fundus glands gradually increased in number in this part, both types of glands being intermingled. Therefore this part may be called the "transitional gland area." In this specimen this transitional gland area on the lesser curvature was 6·5 cm. distant from the pyloro-duodenal border. Even in this area the gland cells of both kinds were never found intermingled in the same gland tubules, which always maintained their independent characteristics of either fundus or pyloric glands. The same condition was found on the transitional area between the pyloric and duodenal glands. The change of the glands here was much more sudden than that between the pyloric and fundus glands. Piersol(2) described it as follows: "The transitional or intermediate zone connecting the pyloric and adjoining portions of the stomach contains forms of glands, those of the fundus variety with parietal cells being intermingled with the pyloric type. Towards the intestine the change of the pyloric glands into those of the duodenum is gradual, the gastric tubules sinking deeper until, as the glands of Brunner, they occupy the submucous coat of the intestine."

The transitional area between the pyloric and fundus glands lies on the small curvature about 1–2 cm. beyond the pyloric ring or incisura angularis, which is 4–5 cm. distant from the pyloro-duodenal border (see fig. 5).

A. (ii) The Adult Stomach (*preserved specimen*)

The distribution areas of both the pyloric and fundus glands were found to be precisely the same as in the fresh specimen.

B. The Stomach of an Infant of six weeks

The total length of the lesser curvature of this stomach after stretching and fixation was about 8 cm. and the length of the entire distribution area of the pyloric glands on the lesser curvature was nearly 3 cm. The ratio between these lengths can be calculated thereupon as 3/8 (approximately 3·8/10 (+)). The width of the "transitional gland area" was about 1 cm., which is comparatively wider than that of the adult. The length of the pyloric gland distribution area on the greater curvature was equal to that on the lesser curvature, so that the distribution area of the pyloric glands in the infant stomach is much larger in proportion, being longer and wider than that of the adult stomach.

The oxyntic cells were found also in the pyloric glands, being fewer in comparison with those in the adult.

The conditions regarding the cardiac glands were the same in the infant stomach as in those of the adult.

The cardiac glands in the human stomach

The glands of the cardia were first described in the kangaroo by Schäfer and Williams (3), in which animal they are simple tubules; and subsequently in various other animals by Ellenberger and Hofmeister (4). The glands of the cardia in man are found by Schäfer (5) to form a zone, which surrounds the cardiac orifice and is generally very small, but may be 3 cm. broad. I have found them in three human specimens in a narrow zone, which was about 0·5 cm. in width as in Piersol's (6) description, being adjacent to the cardiac orifice and forming two to three groups of glands. These secreting gland tubules may be divided into two forms, simple and compound.

The tubules of simple form are composed of moderately high, columnar epithelium, which is filled with granules, always staining intensively with dyes and resembling those of the mucous glands. The gland cells are a little smaller and lower than those of the pyloric and fundus glands.

The cells of the compound forms are found to be of the tubulo-racemose type, resembling rather Brunner's gland of the duodenum than the pyloric. The gland cells are high, columnar and poor in granules. Intermingled with these secreting gland cells are found a few acidophile cells,—especially in the gland body,—which take a parietal position between the ordinary gland cells.

In some animals these glands constitute a much wider zone, as in the hog, in which they occupy almost a third of the entire stomach. It is described by Haane (8) as follows: "Durch Eosin werden die Drüsen der Cardia stark roth gefärbt. Diese Färbung kommt in ihrer Intensität der Rothfärbung der Belegzellen der Fundusdrüse nahe, welche wir an diesen bei Färbung mit Eosin wahrnehmen." These glands are regarded by Oppel as modified fundus glands, since they possess similar epithelium, usually including a

few parietal cells. But I consider that the cardiac gland is an independent kind of gastric gland, having similar epithelium to the pyloric and Brunner's glands and being associated with a few oxyntic cells.

The oxyntic cells and their distribution in the human stomach

(A) *In the pyloric and in the cardiac glands.* The fact that a small number of oxyntic cells are to be seen in the pyloric glands is already described by Nussbaum (9), etc.: "There are also a few isolated cells (Nussbaum), which resemble in structure and in their behaviour to anilin dyes the parietal cells of the fundus glands." Stöhr (10) described it as follows: "Beim Menschen finden sich auch hier (Pylorus) vereingelte Belegzellen, bei Tieren z. B. beim Hunde, einzelne dunklere kegelförmige Zellen, die ihr Aussehen einer durch Nachbarzellen bewirkten Kompression verdanken." Schäfer (11) says: "Amongst the ordinary cells of these glands (pyloric glands) some are here and there found, which stain with osmic acid much more deeply than the rest. The nature and function of these cells,—which were described by Nussbaum,—is not known. They are not identical with the parietal cells of the fundus glands. Occasionally, true parietal cells have been found in the pyloric gland and even in Brunner's glands in the duodenum."

As above described, a few acidophile cells have already been found in the pyloric glands. But it has not been determined, whether they have the same function as those of the fundus glands from a physiological point of view. From the anatomical and the histological standpoint, I cannot find any difference between them, regarding their reaction to dyes, their positions in the glands, their size and form. But there is one and only one difference between them, in the pyloric glands the number of the oxyntic cells is relatively smaller than that in the fundus glands. I consider that these acidophile cells in the pyloric glands and those in the cardiac glands are both of the same nature as those of the fundus; they should be therefore the so-called "oxyntic cells."

The distribution of the oxyntic cells in the pyloric glands was found by me to be as follows. Within a few millimetres of the pyloro-duodenal border, they were very rarely seen, being isolated here and there in the gland body (as was seen in the case of the cardiac glands). They were sometimes found in Brunner's glands of the duodenum. At a distance of 0·5 cm. away from the pyloro-duodenal border, many oxyntic cells were found already in group form, each tubule often containing 15 cells or so. Many secreting tubules were found here without oxyntic cells, which tubules were intermingled with the other tubules containing oxyntic cells. Nearer the transitional area of the pyloric and fundus glands, the oxyntic cells increased in number, so that nearly all the tubules contained more or fewer oxyntic cells, as if they had been one of the physiological and anatomical elements. The number of these cells in this part of the human stomach was incomparably in excess of those in the animals above described. Consequently the results attained from the

experiments made on the animals are not immediately applicable to the study of the secretion of the human pyloric glands.

(B) *In the fundus glands.* In the fundus glands, the oxyntic cells were for the most part numerous in the gastric body and the prepyloric part, especially near and on the lesser curvature. Howell's (12) description of it is as follows: "From a physiological standpoint it is important to remember that the parietal cells are massed, as it were, in the glands of the middle or prepyloric region of the stomach, that they are scanty in the fundus and absent in the pyloric region. This fact is indicated to the eye by the deeper red or brownish colour of the mucous membrane in the prepyloric region." By Grützner (13) it is found that the digestion of foods occurs mostly in the prepyloric part, the food being impregnated first with pepsin and then with acid, and the fundus part being simply a filling organ for the food. He described it as follows: "Nämlich, dass sich der Mageninhalt in ganz gesetzmässiger Weise schichtet, indem der leere Magen, dessen Wände sich berühren, so aufgefüllt wird, dass im allgemeinen die spaeteren Nahrungsmittel in die Mitte der alten gelangen und so zunächst vor der Berührung mit der Magenwand geschutzt werden. Der linke Theil des Magens, der sog. Fundus oder die Pars splenica, ist das eigentliche Auffüllungsorgan. Hier ruhen die Speisen namentlich in der Tiefe stundenlang, ohne auch nur mit Spur Magensaft in Berührung kommen. Während dieser Zeit aber vollzieht sich die Wirkung des Speichels—die amylotische Wirkung. Zu gleicher Zeit, nicht aber durchweg spaeter, wie man bisher glaubte, wird in dem rechten Abschnitt des Magens, dem präpylotische und pylorische Theile, tüchtig peptisch verdaut, indem die hier gelegenen Nahrungsmittel im Verein mit den von rechts her oberflächlich abgewichten und gewöhnlich reichlich mit Pepsin beladenen Nahrungsmitteln mit stark saurem und peptischem Saft durchtränkt und zugleich kräftig durchknetet werden. Auf diese Weise wird der Inhalt grösstenteils verdaut und das verdaute sofort aus dem Magen befördert."

This distribution of the oxyntic cells is very interesting with reference to the digestion of food and the genesis of chronic gastric ulcer. Grützner said: "An jedem Abschnitt der Magenschleimhaut geht streng genommen etwas ander vor, sowohl secretorisch wie motorisch. Die Zusammensetzung des Mageninhaltes ist, wenn man es genau nimmt, nirgend ganz gleich....Man darf deshalb nicht, wie es z. B. Pawlow thut, ein bestimmtes Stück Magenschleimhaut ein seiner Thätigkeit ohne weiteres als das Spiegelbild—wenn ich so sagen darf—der ganzen übrigen Magenschleimhaut, ansehen und den von ihm zu bestimmten Zeiten gelieferten Magensaft dem an anderen Stellen der Magenschleimhaut abgesonderten Saft gleichstellen. Das ist sicher nicht der Fall; der Magensaft in der Regio prepylorica ist sicherlich im Durchschnitt viel sauerer als der aus der grossen Curvatur oder gar der dem Fundus." This is of great importance and contains much valuable information for the study of the genesis of chronic gastric ulcer and of the situations for the formation of different strengths of the gastric

juice in acid and ferments, especially of the gastric acid in connection with the distribution of the oxyntic cells.

Another kind of gastric gland in man

Besides the above described three types of the gastric glands here and there were found a great number of mucous glands, especially near the transitional part of the pyloric and fundus glands. In certain parts of the stomach were found the so-called "true crypts of Lieberkühn," which are similar in all respects to those of the small intestine. These were generally numerous in the transitional part of the pyloric-fundus glands and a few were found quite close to the pylorus and to the cordia. From a physiological point of view it has not been determined what function these islands of the mucous membrane have.

(V) THE RATIOS OF THE DISTRIBUTION LENGTH OF THE PYLORIC GLAND AREA TO THE TOTAL LENGTH OF THE LESSER CURVATURE

Guinea-pig	5/10
Rabbit	7/10
Cat	4/10
Human being (adult)	3/10
„ „ (infant)	4/10

The distribution area of the pyloric glands in herbivora is wider than that in carnivora. Consequently the carnivora have relatively wider distribution area of the fundus glands.

(VI) GENERAL CONCLUSIONS

(1) The distribution area of the pyloric glands can be mathematically determined by describing a circle, its centre being at the pyloric end of the lesser curvature and its radius equal to a certain proportion of the length of the lesser curvature, e.g. 5/10 guinea-pig, 7/10 rabbit, 4/10 cat, 3/10 (adult human), and 4/10 (infant human). The distribution area of the pyloric glands represents that covered by the circle; the distribution area of the fundus glands can be determined from this.

(2) There is no difference between the distribution areas of the gastric glands (pyloric and fundus) on the anterior and posterior walls; so that they are found to be completely symmetrical on the two sides.

(3) The transitional area of the pyloric fundus glands forms a line in the guinea-pig, the rabbit and cat, and is 1 cm. in width in man. The pyloric glands are gradually decreased in number and the fundus glands gradually increased, both types of glands being intermingled; but the gland cells of both kinds are never found intermingled in the same gland tubule.

(4) The distribution area of the pyloric glands in the guinea-pig and

Fig. 6.

Fig. 7.

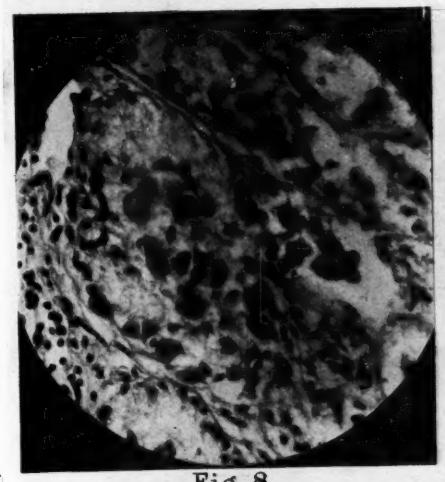


Fig. 8.

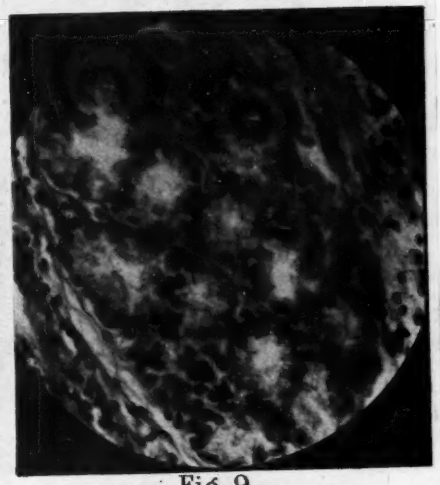


Fig. 9.

rabbit is much wider than that in the cat and man. The cat and man have consequently a comparatively wide distribution area of the fundus glands.

(5) The oxyntic cells from the histological and the anatomical standpoints are always found in both the pyloric and cardiac glands; in the human pyloric glands, they are found especially numerous, as if they were one of its physiological and anatomical elements.

(6) In the fundus glands, the oxyntic cells are most numerous and characteristic particularly in the gastric body and the prepyloric part, and especially near and on the lesser curvature.

(7) The cardiac glands in the above described animals and in man are always found in a narrow area in groups of from two to four, which surrounds the cardiac orifice. But I consider that they are an independent kind of gastric gland.

(8) A great number of mucous glands and so-called "crypts of Lieberkühn" are found here and there.

I desire to express my best thanks to Dr C. Bolton, F.R.S., for his kindness in my research. The expenses have been met by a grant from the Graham Research Fund of the University.

REFERENCES

(1) Haane. *Archiv f. Anatomie*, 1905.
(2) Piersol. *Human Anatomy*, 1918.
(3) Schäfer and Williams. *Proc. Zool. Soc.* 1876.
(4) Ellenberger und Hofmeister. *Arch. f. wiss. u. prakt. Tierheilk.* 1885.
(5) Schäfer. *Quain's Elements of Anatomy.*
(6) Piersol. *Human Anatomy*, 1918.
(7) and (8). Haane. *Archiv f. Anat.* 1905.
(9) Nussbaum, refer. Kemp. *Diseases of the Stomach, Intestine and Pancreas*, 1917.
(10) Stöhr. *Handbuch d. Histologie*, 1906.
(11) Schäfer. *Quain's Elements of Anatomy.*
(12) Howell. *Textbook of Physiology*, 1918.
(13) Grützner. *Arch. f. Physiologie*, von Pflüger, Bd. 106, 1905.

DESCRIPTION OF PLATE III

Fig. 6. Two oxyntic cells in the pyloric gland (guinea-pig).
Fig. 7. Four oxyntic cells in the pyloric gland (rabbit).
Fig. 8. Many oxyntic cells in the pyloric gland (human adult).
Fig. 9. Cardiac gland, simple tubular form (human adult).

PARTHENOGENESIS IN THE WATER VOLE, *MICROTUS AMPHIBIUS*

By G. S. SANSOM, B.Sc.,

Hon. Research Assistant, Dept. of Zoology and Comp. Anatomy, University of London, University College

THERE is already a considerable amount of literature dealing with the segmentation of ovarian ova in the mammalia but authorities are not yet in agreement as to the interpretation of the various conditions obtaining in the ova contained in atretic follicles. It is hoped that the present paper will throw further light on the subject.

In 1899 Bonnet reviewed all the literature dealing with this subject and came to the conclusion that none of the mitoses seen in ovarian ova were cleavage mitoses, but that they were abnormal maturation processes, and that the multicellular eggs described by various workers were purely the result of degenerative fragmentation. Since then Spuler has described mitotic figures centrally situated in ova with one polar body and maintained that they were cleavage spindles, on the ground that ovulation normally occurred prior to this stage of development. He also described one egg with two polar bodies and centrally located spindle. This does afford some evidence in favour of parthenogenesis but the two polar bodies may have been, and indeed probably were, formed by the division of the first. This latter process appears to occur exceedingly frequently in the ova of the Water Vole. Van der Stricht in 1901, working on the ovary of the bat, produced far stronger affirmative evidence of parthenogenesis. He found ovarian eggs with two equal blastomeres yet he interpreted them as oocytes with abnormally large polar bodies. Loeb in the same year figured multicellular eggs with one blastomere dividing mitotically. The spindle was devoid of astral rays and similar in dimensions to a polar spindle and, for this reason, Newman considers this to be a case of polar body formation in an egg undergoing degenerative fragmentation, although in 1913 he himself produced strong evidence in favour of parthenogenetic cleavage in the Armadillo. Rubaschkin in 1906, working on Cavia, came to the conclusion that all mitoses in ovarian ova were more or less abnormal maturation divisions. Athias in 1908 and 1909 also reviewed all the evidence then available and inclined to the negative view. The present author has attempted to give a comparative account of the maturation and cleavage stages occurring in normal eggs and those in atretic follicles, and to show that in *Microtus amphibius* parthenogenesis does occur to a limited extent.

This work was undertaken by me at the suggestion of Prof. J. P. Hill, F.R.S., to whom I am greatly indebted for much valuable assistance and advice.

MATERIAL AND METHODS

The water voles, living in the wild state, were killed during the spring breeding season, March and April, and the ovaries and uteri immediately removed and placed in fixing fluids. Of the latter the following gave the best results: (i) Bouin's Picro Formol Acetic, (ii) a modification of Carnoy's fluid containing 60 per cent. absolute alcohol saturated with mercuric chloride, 30 per cent. chloroform and 10 per cent. glacial acetic.

The ovary of the water vole is completely invested in a tough capsule into the interior of which opens the fimbriated end of the Fallopian tube. The capsule is rich in fat and this rendered the employment of a fixative with great penetrative power necessary.

The ovaries and Fallopian tubes were cut together in serial sections mostly 10μ, some 8μ, in thickness and stained with Erhlich's Haematoxylin or Iron Haematoxylin and Eosine. The plates accompanying this paper were made from photomicrographs for assistance in the preparation of which I am indebted to Mr F. J. Pittock of University College.

NORMAL MATURATION STAGES

A longitudinal section through a mature ovary of *Microtus* is represented in Pl. IV, fig. 1 which shows the investing capsule into the interior of which the ripe ova are discharged on the bursting of the follicles. This ovary was taken from a non-pregnant female killed during the breeding season. Two large ripe follicles and many smaller degenerating ones are present. In the normal ripe follicle the outer wall projects from the surface of the ovary and is exceedingly thin. The ovum, surrounded by cells of the corona radiata, lies free in the liquor folliculi. It is invested in a clear zona, exhibiting no radial canals, to which the corona radiata cells are attached by fine filaments. The ovum possesses a single polar body with scattered chromosomes whilst those of the egg are in a compact group. The diameter of the oocyte is ·048 mm., that of the polar body ·019 mm., the thickness of the zona ·003 mm. Fig. 2 is a high power view of the same egg, the plane of section nearly coincides with the plane of separation of the polar body.

In the same ovary there occurs a similar normal ripe follicle containing an ovum with two polar bodies (fig. 3). The chromosomes in both polar bodies and also in the egg are in compact groups and it seems highly probable that the first polar body has divided into two, since the chromosomes are normally scattered and the two polar bodies present are each considerably smaller than the average first polar body. There are no signs of the second polar spindle.

The next stage obtained was found in the other ovary of the same female.

In this the follicle has burst and the ovum, surrounded by its zona and numerous adherent cells of the corona radiata, is free in the ovarian capsule. This ovum is apparently not yet fertilised and although large numbers of sperms occur in the Fallopian tube none are to be seen in the capsule. Its diameter is ·052 mm., it has a single polar body with scattered chromosomes, whilst those of the oocyte are in a compact group. No spindle is visible. The follicle from which this egg was discharged has a fairly extensive cavity containing comparatively few free follicular epithelial cells. The gap in the follicle wall is closed by a plug of structureless coagulum.

MATURATION STAGES IN ATRETIC FOLLICLES

Follicular atresia has been dealt with very fully by various workers and it is unnecessary to describe it for *Microtus*. The conditions obtaining in atretic follicles agree very closely with those figured by Flemming for the rabbit ovary.

The first polar spindle at the time of its formation lies close to the surface of the oocyte and nearly tangential to that surface. The bivalents have the form of dumb-bell shaped rods arranged in a fairly compact mass on the equatorial plate of the spindle.

During the metaphase the spindle apparently swings round and ultimately comes to lie in a radial position. The chromosomes divide and pass towards the poles of the spindle. The fibres of the latter do not come to a very sharp focus and the whole spindle is usually rather shorter and broader than the second maturation spindle. No cases of spindle fibres splitting and giving rise to pseudoasters, as described by Kingery for the ova of the white mouse, were observed in the case of the water vole. The spindle persists until the polar body is completely constricted off. Fig. 4 shows the separation of the first polar body with the persistent spindle fibres. Immediately the spindle disappears the chromosomes become scattered throughout the cytoplasm of the polar body, fig. 5, as in normal eggs, compare fig. 2. The number of chromosomes, so far as I have been able to determine it, is probably twelve. Those in the polar body vary in size and shape but mostly have the form of pear-shaped rods. The eggs in these follicles vary in size from ·048 to ·074 mm. in diameter, the polar bodies vary from ·02 to ·04 mm. As Van der Stricht has stated, the first polar bodies given off by oocytes in atretic follicles are often far larger than those met with in normal maturing oocytes. According to him they are occasionally the same size as the secondary oocyte itself. This may be the case in *Vesperugo* and *Vespertilio* but it is certainly not so in *Microtus*. In this mammal it is not possible to regard the two-celled eggs met with in atretic follicles as secondary oocytes with abnormally large polar bodies.

The separation of the first polar body probably occurs very rapidly after the formation of the spindle, as large numbers of eggs were found with the first polar body but comparatively few with the spindle alone. On

completion of the first maturation division the nucleus of the secondary oocyte is not reconstituted, the chromosomes remaining in a compact group until the formation of the second spindle. This agrees with the conditions which obtain in normal oocytes as represented in fig. 3.

In a large number of cases the first polar body exhibits signs of mitotic division prior to the formation of the second polar spindle. Spindle fibres make their appearance in the cytoplasm of the polar body, sometimes irregularly arranged as in fig. 6, sometimes in typical form as in fig. 7.

The chromosomes appear irregularly arranged along the fibres but soon separate into two well defined groups and the polar body divides into two. In fig. 7 the first polar body is in process of division, while in fig. 8 the division is completed and the second polar spindle formed. The latter almost invariably appears nearly radial in position; with one pole directed towards the periphery of the first polar body. It is usually longer and narrower than the first spindle and its fibres come to a sharp focus. Pl. V, fig. 9 represents it typically, with the chromosomes arranged in an equatorial plate. Its length is about ·022 mm. and its diameter ·004 mm.

No stages have been obtained showing the completion of the second maturation division either in normal eggs or in ovarian eggs contained in atretic follicles. This agrees with Van der Stricht's observations: "Jamais il ne nous a été donné d'observer le détachement d'un second globule d'un œuf à l'intérieur de l'ovaire, pas même d'oocytes de second ordre en apparence normaux, retenus dans un follicule dont la déhiscence ne s'est pas opérée."

All the eggs described above resemble one another in size and in optical and staining properties, the normal ovum and that from a follicle in the early phase of atresia being indistinguishable. The condition of the follicular cells however enables one to say whether the follicle is normal or in process of atresia.

The first signs of atresia are characteristic changes in the cells of the membrana granulosa and discus proligerus. Some of these cells lose their connection with the remainder, become rounded off and their nuclei stain intensely black with haematoxylin. They float free in the liquor folliculi and have been described by various workers as phagocytic in character. A comparison of figs. 2 and 3 with figs. 5 and 6 clearly demonstrates these typical changes.

Some of the atretic ova are devoid of a zona while others possess it, but the presence or absence of a zona pellucida around an egg is conditioned by the fixing agent employed. In ovaries fixed in Bouin's fluid it is sometimes present, more often absent, while in those fixed in Carnoy Corrosive Mixture or any other fixative containing mercuric chloride it is invariably present.

In a few atretic eggs there occurs in the cytoplasm a small spherical body staining deeply with eosine. It possibly represents the yolk nucleus of Balbiani.

CLEAVAGE OF NORMAL EGGS IN THE FALLOPIAN TUBE

No stages are available of fertilisation or of ova with male and female pronuclei. The first normal stage in the cleavage process obtained is that of the two-celled egg represented in fig. 10. Two equal blastomeres are present, apparently identical in character and size, still surrounded by a thick intact zona, inside of which there is no sign of the polar bodies. This egg measures ·054 × ·045 mm. in diameter, the thickness of the zona is ·003 mm. Both nuclei are centrally situated and in the resting condition. Several two-celled stages were obtained, all very similar to the one figured. In none of them are there present any definite polar bodies, but in one there are certainly indications of the presence of possible remnants of the same in the cleavage plane of the egg.

The next normal stage obtained is an eight-celled egg lying free in the upper portion of the uterus. The zona is still present and almost intact. No polar bodies are present. All the cells and their nuclei appear similar, the latter being in the resting condition. The diameter of the egg is ·074 × ·053 mm.

Two 13-celled stages were obtained, in one the egg measured ·074 × ·056 mm. It is completely surrounded by a zona and consists of twelve blastomeres arranged peripherally and one central cell, which is not recognisably different in character from the others, and which reaches the surface on one side. This suggests the occurrence of a process of epibole or overgrowth. It is possible this central cell has not divided since the second cleavage and that the mode of arrival at the present number of blastomeres is as follows:

$$1 \rightarrow 2 \rightarrow 3 + 1 \text{ (future central cell)} \rightarrow 6 + 1 \rightarrow 12 + 1 \text{ central cell.}$$

CLEAVAGE OF OVARIAN EGGS

The first cleavage occurs in a plane at right angles to the plane of separation of the polar body. Fig. 11 is a drawing of a section through an egg contained in a small atretic follicle. This egg has no investing zona but the vitelline membrane is well defined. Two polar bodies are present one much larger than the other. The chromosomes in the smaller are in a compact mass, in the larger a resting nucleus has been reconstituted (fig. 8). The sectional plane coincides with the plane of separation of the polar bodies and also with the long axis of the cleavage spindle, i.e. the first cleavage is at right angles to the plane of separation of the polar bodies. This cleavage spindle is far larger than a polar spindle; it measures ·03 mm. in length and ·007 mm. in diameter. The fibres come to a sharp focus, centrosomes are probably not present, astral radiations are certainly absent. The chromosomes are arranged irregularly along the spindle fibres, they have the form of thick curved rods. The egg cytoplasm is not homogeneous, it contains several very granular areas staining more deeply with eosine, and around the outer thirds of the spindle are two spherical clear areas of cytoplasm.

Spuler in 1901 and Newman in 1913 both figured cleavage spindles with centrosomes and astral radiations and laid special emphasis on the fact that asters are never associated with maturation spindles. In the egg represented in fig. 11 there are certainly no asters visible yet it seems far less probable that the spindle is a second polar spindle than that it is a cleavage spindle. Its length is ·03 mm. and its diameter ·007 mm. whereas the second polar spindles vary in length from ·02 to ·015 mm. and in diameter from ·005 to ·004 mm. No second polar spindles occur centrally situated, they are invariably close to the surface, with one polar directed towards the margin of the first polar body or its daughter cell. This spindle is not only central but lies in a plane almost parallel to the plane of separation of the polar bodies. Moreover in all the numerous ovarian eggs exhibiting second polar spindles which I have examined the chromosomes are situated in a compact mass on the equatorial plate, whereas here they are scattered irregularly along the fibres.

It seems highly probable that in the parthenogenetic development of ovarian eggs the second polar body is suppressed, the second polar spindle either degenerating or being converted directly into the first cleavage spindle.

The completion of the first cleavage in an ovarian egg is represented in fig. 12. The egg is lying free in the liquor of the atretic follicle. It is invested in a zona and consists of two equal blastomeres with resting nuclei. One or possibly two small polar bodies are situated inside the zona in the cleavage plane. At the opposite side is a non-nucleated body which is probably deutoplasmic in character, the extrusion of such deutoplasmic material by segmenting eggs being not improbable. This egg measures ·056 × ·051 mm. in diameter.

No stages with the second cleavage spindles were obtained, but in one two-celled egg the nucleus of one of the blastomeres has divided unequally into two, one large, and one quite small, daughter nucleus being formed, the plane of division being at right angles to the first cleavage plane. Lying inside the zona in the cleavage plane are two small non-nucleated bodies which may be deutoplasmic or may be the remains of the polar bodies.

Mention may be made here of a two-celled stage found in the ovary of the mouse. This egg, represented in fig. 16, which is a reproduction of a beautiful drawing by the late F. J. Bridgman of University College, is actually in process of division. Unfortunately Mr Bridgman left no description of this stage and the original slide from which the drawing was made is not available. Apparently the conditions obtaining are very similar to those described for *Microtus*. One polar body with scattered chromosomes is present. The clear areas of cytoplasm around the ends of the spindle as in fig. 11 are very marked and the general characteristics of follicular atresia are well shown.

The completion of the second cleavage in a plane perpendicular to the first and to the maturation division is shown in fig. 13 which represents a section through a four-celled stage. This egg has a diameter of ·059 mm.

The zona has disappeared and no polar bodies are recognisable. The four blastomeres are grouped in two pairs showing the typical cross-shaped arrangement. One pair is larger than the other. Each blastomere possesses a large nucleus in the resting condition, but in addition several small supernumerary nuclei are present. At one pole are two small non-nucleated bodies, which are probably of a deutoplasmic character.

Another four-celled stage occurs in the same ovary. In this the blastomeres are differently arranged to those in the preceding egg. Three of them lie in one plane, the dividing lines being radial and meeting at 120° in the middle, the fourth blastomere lies in a plane parallel to that of the other three and occupies the entire opposite pole of the egg, the whole forming a pyramid. Several small supernumerary nuclei are present close to the normal nuclei, two of them possess discreet chromatin masses. A small non-nucleated, probably deutoplasmic, body is present at the outer junction of the three symmetrical blastomeres. This egg, represented in fig. 14, measures ·063 × ·056 mm.

No egg with more than four blastomeres was found in atretic follicles. A large number of eggs undergoing degenerative fragmentation occur in nearly all the ovaries examined, but these are entirely different in character from the segmenting parthenogenetic eggs described above, and are dealt with in the next section.

DEGENERATIVE FRAGMENTATION

The above heading is the term adopted by many writers to cover the parthenogenetic cleavages of ovarian eggs.

Janosik, however, in 1897 described in the rabbit and guinea-pig two entirely different conditions obtaining in dividing ovarian eggs.

"4. Es kann die Theilung aber auch zur Bildung von Segmenten führen, welche untereinander ungleich gross sind, die aber alle Kerne besitzen und somit den Charakter von Zellen haben. 5. Neben diesen wirklichen Theilungen kommen auch vielfach nur Fragmentirungen der Eizelle vor (welchen Vorgang man besonders bei älteren Thieren vorfindet) oder es kann auch die Eizelle schollig zerfallen."

These two conditions which Janosik described also occur in the ovary of the water vole, and some of the preparations figured by him bear a striking resemblance to some of mine. Compare fig. 14 in this paper with Janosik's fig. 5. There seems little doubt that Janosik's material was very similar to my own, though he found ovarian eggs with many more blastomeres than have been seen in *Microtus*. He also described and figured small bodies in contact with the blastomeres of the three and four-celled stages and interpreted them as polar bodies, it seems probable however that some of them were deutoplasmic in origin.

The cleavage stages represented in figs. 12, 13 and 14 bear little resemblance to eggs which are obviously undergoing degenerative fragmentation. The

latter have been described very fully by various workers, Flemming in 1885 and Kingery in 1914, and it is unnecessary to describe them in detail for the water vole, suffice it to say that fragmenting eggs have quite distinctive characters. The zona, which is nearly always present, stains very deeply with eosine as does the egg cytoplasm. The latter contains several (in late stages many) small nuclei and a variable number of cells characterised by intensely dark staining nuclei and scanty cytoplasm. These cells may be formed inside the egg, but are more probably wandering phagocytic cells from the follicular epithelium. The contents of the egg in fact resemble a syncytium, the cytoplasm of which may fragment into a number of irregularly shaped pieces with or without nuclei. Distinct cell walls such as are visible in figs. 12, 13 and 14 never occur in these fragmenting eggs and mitotic figures also are invariably absent. Fig. 15 represents a typical degenerating egg. It is not possible to determine whether such eggs, prior to their present condition, were undergoing parthenogenetic cleavage or not but owing to the comparative scarcity of cleavage stages it is safe to assume that the majority of eggs undergoing degenerative fragmentation never completed their first cleavage.

SUMMARY

From a study of the ovary in the water vole one is led to believe that true parthenogenesis does occur to a limited extent and that it is quite distinct from the degenerative processes which result firstly, in the production of multinucleate masses and secondly, fragmentation of the cytoplasm. This is the fate of all eggs which either fail to reach maturity owing to the unfavourable situation of the follicle in the ovary, leading to insufficient nutrition, or which reach maturity but fail to be discharged from their follicles owing to lack of the requisite stimulus to cause ovulation. Whether or not ovulation can take place independently of copulation in *Microtus* is uncertain but it seems improbable. Some mature females killed during the height of the breeding season were not pregnant and examination of their ovaries showed that all the larger follicles were undergoing atresia and that the Fallopian tubes contained no sperms. Some of the accompanying figures are made from ovaries of non-pregnant females killed during the breeding season, but the same phenomena are met with in the ovaries of pregnant females and of those which have recently given birth to young. Unfortunately only one stage was obtained of the ripe ovum immediately after ovulation and in this case sperms were present in the tubes. The evidence though slight therefore favours the view that ovulation only occurs after copulation.

The course of events in this parthenogenetic development appears to be as follows. The vitality of an egg enclosed in an atretic follicle persists for a variable time and, despite the fact that the follicle contains an enormous number of degenerating cells, enables the egg to carry out the earlier stages of development. The first polar body is separated off and divides mitotically into two unequal portions, the second polar spindle is formed but owing to

lack of the stimulus normally afforded by penetration of the sperm, the second polar body fails to separate. The first cleavage spindle then arises either from the second polar spindle or *de novo*, and the first cleavage takes place, resulting in the formation of two equal blastomeres in a plane at right angles to the plane of separation of the first polar body. These two blastomeres then divide giving rise to the four-celled stage. Meanwhile the blastomeres eliminate a variable number of small deutoplasmic bodies which together with the polar body are absorbed or destroyed by the follicular cells. By this time the conditions of atresia in the follicle are so acute that further development is impossible. Cytolysis, nuclear degeneration and fragmentation set in, probably hastened by penetration of phagocytic cells, with the result that the degenerating egg comes to consist of a deeply staining mass, imbedded in which are numbers of more or less degenerate nuclei. In the great majority of eggs the atresia gains the upper hand long before the first maturation division is completed.

Newman (1913) states that the parthenogenetic cleavage stages, which he found in the Armadillo, were probably not preceded by maturation divisions, no polar bodies being given off from those eggs destined to undergo parthenogenetic development. He gives no reasons to support this view and in the case of *Microtus* such suppression of the first polar body certainly does not occur, though as already stated the second polar body is probably not extruded by unfertilised eggs. There is a reasonable explanation, whether sound or not I cannot assert, for suppression of the second polar body, but it is difficult to find a satisfactory one to account for the absence of the first.

Janosik (1897) stated that in his opinion such parthenogenetic development probably occurred in unfertilised ova in the Fallopian tube. No such stages have been observed in *Microtus*. It might be mentioned that one egg was found in the upper part of the Fallopian tube of a female killed shortly after parturition. It is surrounded by a thin zona, entirely free from any corona radiata cells and possesses a single small polar body with chromosomes in a compact mass, while those of the ovum are thin curved rods closely grouped together. The condition of the follicle from which it was shed suggests that ovulation occurred some days previously. No sperms are present in the Fallopian tube. If parthenogenesis occurs in the Fallopian tube, it might well have happened in this case.

Precise information as to the breeding habits of the water vole is not available, but it seems probable that after the spring breeding season there is a resting period of several months.

REFERENCES

ATHIAS. "Les phénomènes de division de l'ovule dans les follicules de De Graaf en voie d'atrésie." *Anat. Anz.* Bd. XXXIV. 1909.

BONNET. "Giebt es bei Wirbeltieren Parthenogenesis?" *Erg. Anat. u. Ent.* Bd. IX. 1899.

FLEMMING. "Ueber die Bildung von Richtungsfiguren in Säugethieren beim Untergang Graaf-schen Follikel." *Archiv f. Anat. u. Phys. Anat. Abth.* 1885.

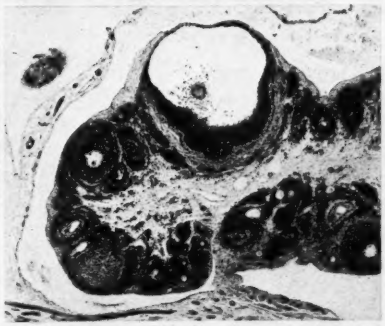


Fig. 1.

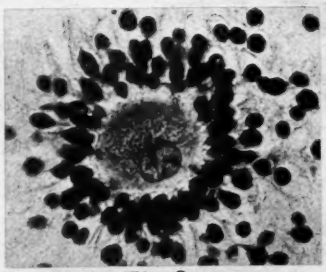


Fig. 2.

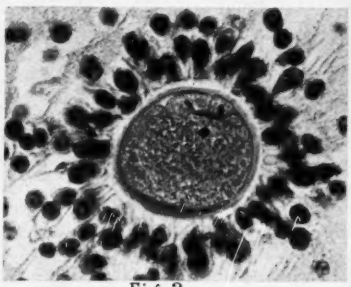
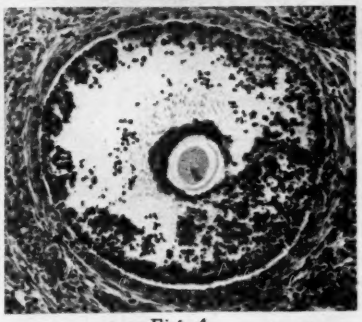


Fig. 3.



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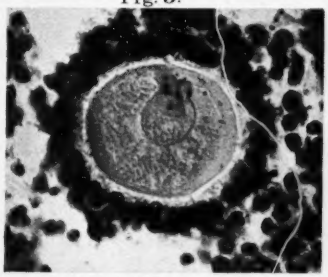
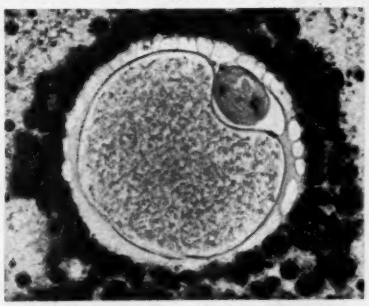


Fig. 5.



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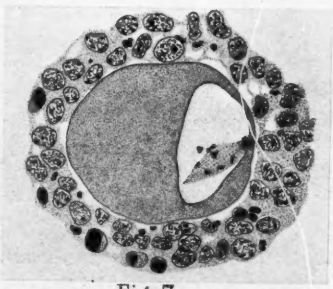

Fig. 7.

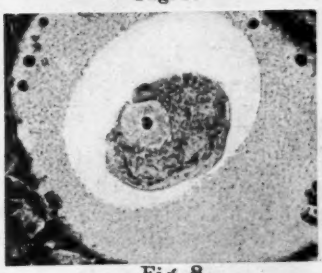

Fig. 8.

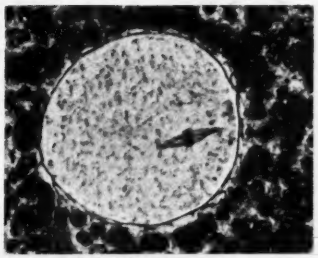

Fig. 9.

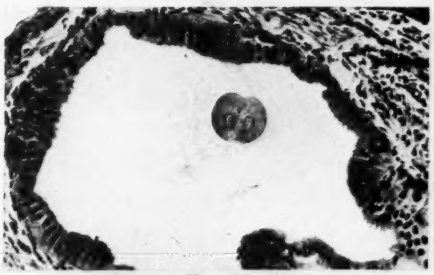

Fig. 10.

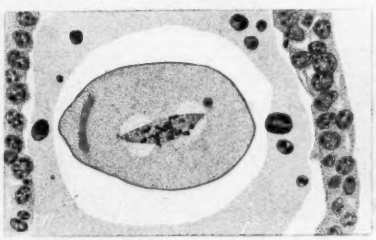

Fig. 11.

Fig. 12.

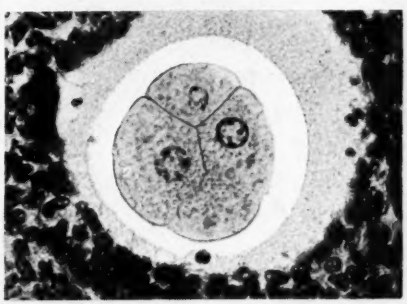

Fig. 13.

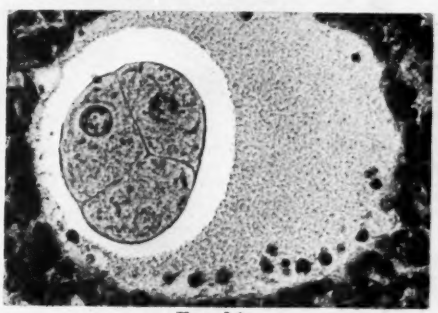

Fig. 14.

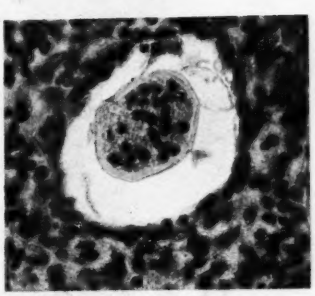

Fig. 15.

Fig. 16.

HEAPE. "Ovulation and Degeneration of Ova in the Rabbit." *Proceedings of the Royal Society*, vol. 76 B, 1905.

JANOSIK. "Die Atrophie der Follikel." *Archiv f. Mikros. Anat.* Bd. XLVIII. 1897.

KINGERY. "So-called Parthenogenesis in the White Mouse." *Biological Bulletin*, vols. XXVII. and XXVIII. 1914 and 1915.

KIRKHAM. "Maturation of the Mouse Egg." *Biological Bulletin*, vol. XII. 1907.

KIRKHAM and BURR. "Breeding, Maturation and Ovulation in the White Rat." *American Journal of Anatomy*, vol. XV. 1913–1914.

MARSHALL. *The Physiology of Reproduction.*

NEWMAN. "Parthenogenetic Cleavage of the Armadillo ovum." *Biological Bulletin*, vol. XXV. 1913.

RUBASCHKIN. "Über die Veränderungen den Eier in den Zugrunde gehenden Graafschen Follikeln." *Anat. Hefte*, Bd. XXXII. H. 97, 1906.

SCHOTTLÄNDER. "Ueber den Graafschen Follikel u. Beitrag zur Kenntniss der Follikelatresie." *Archiv f. Mikros. Anat.* Bd. XXXVII. 1891 and Bd. XLI. 1893.

SOBOTTA. "Die Befruchtung u. Furchung des Eies der Maus." *Archiv f. Mikros. Anat.* Bd. XLV. 1895.

—— "Die Bildung der Richtungskörper bei Maus." *Anat. Hefte*, Bd. XXXV. 1907.

SPULER. "Über die Teilungserscheinungen der Eizellen in degenerierenden Follikeln des Säugerovariums." *Anat. Hefte*, Bd. XVI. H. 51, 1901.

VAN DER STRICHT. "L'atrésie ovulaire et l'atrésie folliculaire du follicule de De Graaf dans l'ovaire de chauve-souris." *Verhand. d. Anat. Gesellsch.* 15 Versamml. Bonn, 1901.

EXPLANATION OF PLATES IV, V

Fig. 1. Photomicrograph of longitudinal section through the ovary of a mature female, killed just prior to ovulation. One large ripe follicle is visible. Magnified 30 diameters.

Fig. 2. High power view of ripe ovum from the follicle shown in fig. 1. Ovum, surrounded by follicular cells, possesses first polar body with scattered chromosomes. ×500.

Fig. 3. Normal ripe ovum surrounded by follicular cells. The first polar body has divided into two. The second polar spindle has not yet formed. ×500.

Fig. 4. Large follicle in the early phase of atresia. Some cells of the membrana granulosa have broken away from the follicle wall and lie free in the liquor folliculi. The egg exhibits the first polar spindle, the first polar body is in process of extrusion. ×200.

Fig. 5. Atretic follicle containing an egg with first polar body. The chromosomes of the first polar body are scattered. ×500.

Fig. 6. Atretic follicle containing an egg with first polar body. The latter is in process of division, the chromosomes are in two groups and the cytoplasm shows irregularly arranged spindle fibres. ×500.

Fig. 7. Line drawing made with camera lucida, of section through the egg shown in fig. 9. The first polar body possesses a typical spindle and is in process of division. ×750.

Fig. 8. Section through an egg contained in a small atretic follicle. The first polar body has divided into two unequal portions, the larger of which contains a resting nucleus. This egg possesses the first cleavage spindle (see fig. 11). ×450.

Fig. 9. The second polar spindle of an egg contained in an atretic follicle. This egg has a first polar body in process of division (fig. 7). ×500.

Fig. 10. Section through the Fallopian tube of a pregnant female. Typical normal two-celled egg, enclosed in its zona. ×220.

Fig. 11. Line drawing made with camera lucida of egg contained in a small atretic follicle. The first cleavage spindle is present. A section through the same egg is shown in fig. 8. ×630.

Fig. 12. Section through a two-celled egg in an atretic follicle. The zona is still intact. ×500.

Fig. 13. Section through a four-celled stage in an atretic follicle. The four blastomeres lie in one plane with a typical cross-shaped arrangement. One nucleus is not in the sectional plane. ×500.

Fig. 14. Section through a four-celled stage in an atretic follicle. Three blastomeres occupy one plane, the fourth occupies the opposite pole of the egg. ×500.

Fig. 15. Section through an egg undergoing degenerative fragmentation. The zona is still intact but the egg consists of a multinucleate deeply staining mass, exhibiting no trace of cell walls. ×450.

Fig. 16. Line drawing of a section through an atretic follicle of the mouse. The ovum is in process of division into two. The cytoplasmic division is not yet completed. One polar body is shown. The original drawing was made by the late F. J. Bridgman of University College, London.

REVIEWS

Selected Lectures and Essays (including Ligaments, their Nature and Morphology). By Sir JOHN BLAND-SUTTON. 4th edition, pp. 309, figs. 111. Price 15*s*. (London: Heinemann. 1920.)

Sir John Bland-Sutton was one of the original members of the Anatomical Society of Great Britain and Ireland and did much, during the earlier years of its existence, to further its life and prosperity. Many of its members regretted that a busy professional life made it necessary for him to resign his connection with the society. The present volume will show his former colleagues that his interests in anatomical pursuits are still alive and fruitful at the end of forty years spent at the Middlesex Hospital as student, anatomist and surgeon. The opening essays, on the Nature of Ligaments, are already well known to anatomists and need no comment here. In the essays and lectures which follow, such as those on peculiar mechanisms in the orbit, on the structure of the gizzard and ruminant stomach, on misplaced and missing organs and on hermaphroditism he has original observations to record and inferences to draw. We note that the evidence he has collected points to the ovum being transmitted along the Fallopian tube, not by the action of cilia lining it, but by the contraction of its muscular walls. The essays are written in the clear, incisive, piquant style which characterises everything that Sir John Bland-Sutton has written. The essays are illustrated by 111 illustrations drawn and engraved on wood.

The Principles of Anatomy as seen in the Hand. By FREDERIC WOOD JONES, D.Sc., M.B., Professor of Anatomy in the University of Adelaide. pp. 325, 2 plates and 123 text-figures. Price 15*s*. (London: Churchill. 1920.)

In this work Prof. Wood Jones has used the structure of the hand as a means of exemplifying the principles underlying the construction of the human body and has thereby provided medical students with an excellent introduction to their anatomical studies and teachers of anatomy with new facts and novel interpretations of structural problems. He is known to the readers of this Journal as a gifted draughtsman and has illustrated this work by 123 of his original drawings. All through the work the essential primitiveness of the structural characters of the human hand is emphasised while the complexity of its nervous machinery is acutely realized and graphically described. This volume is one which should be on the book-shelves of every thinking anatomist.

The X-Ray Atlas of the Systemic Arteries of the Body. By H. C. ORRIN, O.B.E., F.R.C.S. (Ed.). Large Quarto, with Text and 33 original illustrations. Price 13*s*. 6*d*. net. (London: Bailliere, Tindall and Cox. 1920.)

The author of this atlas while engaged at a military hospital as civil surgeon felt the need of plates which would depict the distribution and relationship of the arteries of the body as revealed by the aid of X-rays. The excellent plates published in this atlas were prepared by the author to meet this need. With one exception all of them are taken from a very successfully infected full-time foetus. The atlas has been prepared for the use of students of anatomy, surgical anatomy and operative surgery, but one would also commend it to the notice of teachers and investigators for some of the plates bring out certain facts—particularly in the course and distribution of abdominal arteries—which are worthy of further study. A useful series of stereoscopic radiographs are added at the end which should prove very serviceable. The price seems to us extremely moderate.